# THE BIOLOGICAL CONTROL OF AN INSECT IN FIJI

## An Account of the Coconut Leaf-mining Beetle and its Parasite Complex

BY

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No. 38246
20 MAY 1937
COIMBATORE

LONDON
THE IMPERIAL INSTITUTE OF ENTOMOLOGY
41, Queen's Gate, S.W. 7
1937

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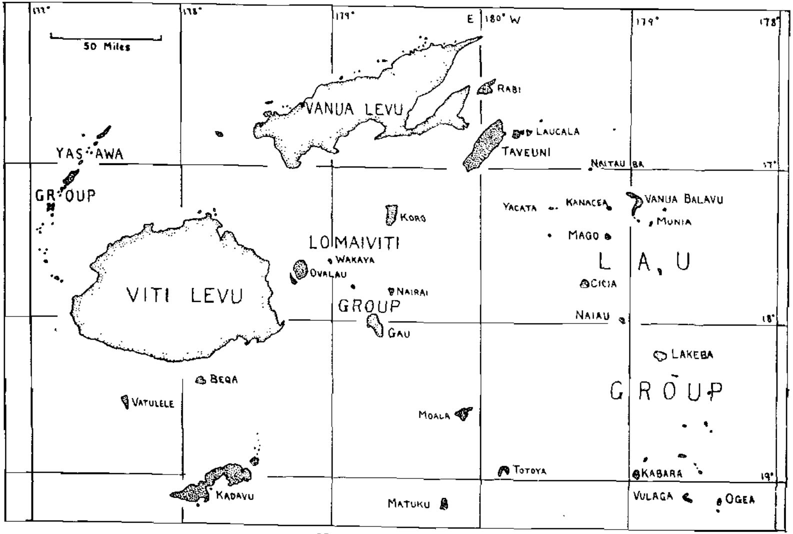


Map 1. The Fiji Islands.

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## I. INTRODUCTION.

In 1924 a Committee was appointed in Fiji to investigate the possibilities of controlling *Levuana iridescens*, B.B., a Zygaenid moth which was at that time a severe menace to the coconut industry of the Colony. The recommendations of this Committee resulted in the appointment of Dr. J. D. Tothill, as Director of the Levuana Campaign, and of Mr. R. W. Paine and the present writer as assistants; and on his arrival in Fiji, Dr. Tothill became chairman of the Committee. Investigations were commenced early in 1925, and in little more than a year the pest was completely suppressed by a Tachinid parasite, *Ptychomyia remota*, Ald., which was introduced from Malaya. The control exercised by this parasite has proved absolutely permanent, and an account of the work was published by the Imperial Bureau (now Institute) of Entomology in 1930.* on behalf of the Government of Fiji.

In 1926, the Committee decided to extend its activities considerably, mainly in the direction of attempting the biological control of certain other serious coconut pests. The first of these other pests to be investigated was the scale-insect, *Aspidiotus destructor*, Sign., which was effectively controlled in 1928 by the introduction from Trinidad of a predatory Coccinellid beetle, *Cryptognatha nodiceps*, Sic. This control also has proved permanent, and an account of the campaign against *A. destructor* was published in 1935 in the *Bulletin of Entomological Research*.†

In 1929, Dr. J. D. Tothill was appointed Director of Agriculture, Uganda, and from that time, until 1934, the entomological work of the Committee in Fiji was continued by his two former assistants, in accordance with a programme drawn up by him before his departure. One of the pests which remained to be controlled was the Leaf-mining Beetle, *Promecotheca reichei*, Baly; and the purpose of this publication is to present an account of the campaign against *P. reichei*, which was the third coconut pest in Fiji to be suppressed by biological methods. The investigation of this Hispid was commenced in 1929, when a detailed study of a severe outbreak on the island Vanua Balavu was undertaken by the present writer. This study served to reveal the type of parasite which was required for the control of *P. reichei*. In 1930, R. W. Paine found time, in the course of other work, to make a preliminary survey of the parasites of an allied species of *Promecotheca* in Java, but apart from this, no further progress was made during 1930 or 1931, the pressure of other work necessitating postponement. At the end of December, 1931, however, the writer arrived in Java to commence a detailed investi-

* Tothill, J. D., Paine, R. W., and Taylor, T. H. C., "The Coconut Moth in Fiji."

† Taylor, T. H. C., "The Campaign against *Aspidiotus destructor* in Fiji." —*Bull. Ent. Res.* **26**, 1–102.

gation of the parasites found in that country by Paine, and this investigation was continued throughout 1932 and until April, 1933, when parasites were shipped from Java to Fiji, one of the Java species having been found suitable, theoretically, for fulfilling the required conditions in Fiji. This parasite suppressed the pest rapidly and most effectively. It was too early, at the time of writing (December, 1934), to be absolutely certain that the control will be permanent, but there are good reasons, which will be discussed later, for believing that the results of the introduction of this parasite will be as permanent as those of the two earlier campaigns.

The case of *P. reichei* proved to be one of peculiar interest. In the first place, the insect is indigenous in Fiji, and there is a vague, but prevalent, belief that an insect is much more difficult to control biologically in its native environment than elsewhere. For this belief, however, there is no justification, except in a few special instances. In the second place, *P. reichei* has its own indigenous primary and secondary parasites in Fiji, and the interrelations of these with one another, and with their host, are such that an economically satisfactory equilibrium is, and always has been, maintained in all normal circumstances. In comparatively recent years, however, an entirely foreign factor, in the form of the mite, *Pediculoides ventricosus*, Newp., has made its appearance and has interfered so extensively with the natural equilibrium that the indigenous parasites have become almost useless, economically, in certain parts of Fiji, and *P. reichei* has acquired the status of a pest. The mite has made it a pest, and has done so, not by elimination of the indigenous natural enemies by direct attack, but by periodic elimination of all developmental stages, except one, of *P. reichei* itself, thus causing and maintaining a condition comparable to that of insects in temperate countries, where development and time of occurrence are controlled by seasonal climatic changes, and successive generations cannot appreciably overlap. The native parasites proved ill-adapted for coping with this new condition, being unable, so long as it prevailed, to multiply continuously. *P. reichei* anomalously became a pest in the presence of the very parasites that normally controlled it. It was evident that, in these very special circumstances, the problem of restoring the insect, biologically, to a state of economic harmlessness necessitated the discovery of a parasite capable of satisfying requirements of an unusually rigid and exacting nature. For these reasons, the problem was one of special interest, and one which, if successfully solved, would be likely to be useful as a demonstration of the wide possibilities of the biological method of control. That the possibilities of this method are far wider than is generally believed, there is no doubt, and this book is written, not merely as a record of a single experiment, but also in the hope that it may prove a useful contribution towards a more thorough understanding of the interrelations of parasites and their hosts, and of the possibilities of the biological method in general. To this end the various sections are arranged, as far as possible, so that they form a consecutive account of the campaign. The earlier sections explain the activities, from both the biological and the economic points of view, of the pest itself and of all the natural enemies present in Fiji at the time of com-

The cost of publication has been met in part by grants from the Royal Society and the University of London, whose generosity the Author desires very gratefully to acknowledge.

Thanks are also due to the Imperial Institute of Entomology for undertaking the editing and production of the work.

## II. *PROMECOTHECA REICHEI*, BALY.

### A. Food Plants.

The normal food for both adults and larvae of *P. reichei* is the leaf of the coconut palm. In most of the localities where *P. reichei* occurs there are no other species of palm. Occasionally, however, this Hispid attacks palms of the genera *Pritchardia* and *Livistona* planted for ornamental purposes. Probably a variety of thick-leaved palms would be attacked if they were available, but there is no doubt that the great majority of species, especially those with thin leaves, would prove immune.

### B. Distribution and Mode of Occurrence.

*P. reichei* inhabits, and is indigenous in, Fiji, Samoa, and Tonga, and this appears to be the limit of its range.*

In Fiji it is present on all the larger islands and most of the small ones. It is never uniformly distributed, however, over any island, and is normally a rare and very local insect. It is usually to be found in only a few widely separated localities on each island, and in each locality it usually disappears soon after it has begun to multiply in a few adjacent trees, natural factors suppressing it completely.

In certain circumstances, however, it multiplies enormously, so that it is present in thousands in every coconut palm over wide areas, and does great damage on the coconut estates concerned. These severe outbreaks occur more frequently in the Lau group than elsewhere and are the principal reason for the present detailed study of the insect; but they cannot be regarded as a normal mode of occurrence for the species because they are usually caused by factors which have arisen as a result of the development of trade and of the commercialisation of the coconut. Prior to the invasion of the islands by white men, *P. reichei* was undoubtedly rare and local, being effectively controlled by its indigenous natural enemies and never multiplying sufficiently to cause too much damage to the coconut palms, except after hurricanes. The equilibrium maintained by the natural enemies was constant over any one large island as a whole, but unstable and wave-like in each locality. The insect was usually comparatively rare even at those times when it reached its maximum abundance in any one locality, but sometimes it was sufficiently abundant at such times to cause slight damage to a few adjacent trees. It showed no tendency to spread, in normal years. Successive generations overlapped completely throughout the year, so that all stages were present simultaneously. This must be regarded as the normal mode of occurrence, and on most islands in Fiji, other than those of the Lau Group, the insect still occurs in this way.

* Futuna and Wallis Islands, between Fiji and Samoa, are included in its range.

## C. Habitat.

The coconut palm grows on the sea-shore. The sea is the medium of distribution of its fruits, which float in the water and are carried by currents to other islands, where they are thrown up on the beaches by the surf. The palms grow close together, if undisturbed, so that their leaves form an almost continuous roof over other vegetation. They thrive on flat coral islands; and on larger, hilly, islands, they flourish not only on the extensive coastal flats, where they form a continuous belt, but also in the small coastal pockets bounded by steep slopes. They receive the full force of gales from the sea, and at certain seasons their leaves are constantly lashed by the wind and covered with salt spray, to which they are very resistant. A coastal belt of coconut palms on a hilly island is visible from a long distance out to sea as a narrow, bright green, line just above the water.

The crowns of coconut palms are the natural habitat of all stages of *Promecotheca reichei*. The insect therefore lives above the level of almost all other vegetation growing in the areas where its food-plant thrives. It lives, in fact, in a layer of coconut leaves many yards above the ground, so that its food is always present and it seldom meets with anything else. In this layer it is very exposed to the sun and to the wind.

The extensive planting and cultivation of coconut palms inland in comparatively recent years has greatly extended, and changed in many other ways, the habitat of *P. reichei*. Many islands, on which the palms were formerly confined to a narrow belt all round the coast, are now almost entirely covered with them. *P. reichei* can now find abundant food in localities where there was formerly no food for it—on the slopes of high hills, and even at their summits, as well as in sheltered inland valleys. The coastal belts of coconuts are greatly widened in many places, and where the palms are properly cultivated, they are more widely spaced than in their natural state and the vegetation beneath them is greatly reduced.

## D. Climatic Conditions.

The climate of Fiji is tropical, but not extreme in any respect. There are two seasons, the hot or wet season and the cool or dry season, but these vary considerably in duration and cannot be sharply delimited. In the former, which usually extends from November to April, inclusive, the wind is very variable but mainly easterly with a northerly tendency. In the latter season, which usually extends from May to October, inclusive, the wind is also mainly easterly, but less variable and with a southerly tendency, while often, for many days, a strong and steady trade-wind blows from the south-east or east. Hurricanes are liable to occur in the hot season, but are comparatively rare events.

The humidity, as is to be expected in a group of comparatively small islands, is fairly high throughout the year and seldom liable to extreme changes. The monthly mean usually lies between 70% and 85% in all coastal localities throughout the year. The humidity is very seldom

below 60% or above 95%, and although there is a higher mean in the hot season, the seasonal change is very slight.

The mean monthly temperature $\left(\frac{\text{max.} + \text{min.}}{2}\right)$ for the hotter months is about 82° F. and for the cooler months about 73° F. The mean monthly maxima and minima in the hotter months are abont 87° F. and 76° F. respectively, and in the cooler months about 78° F. and 68° F. respectively. The daily range in temperature is usually about 10° F.. and the temperature is rarely above 92° F. or below 66° F.

The rainfall is the most variable of the climatic factors, both as regards localities and times of the year. The Lau Group has a much smaller rainfall than the rest of Fiji, considered as a whole, but in the latter there are on the two largest islands (Viti Levu and Vanua Levu) marked wet and dry zones, and in the dry zones, which are leeward coastal belts, the rainfall is similar to that of Lau. The locality with the highest mean annual rainfall is Salialevu on Taveuni, the figure for this locality being 213 ins. The localities with the lowest mean annual rainfall are Navo and Lautoka on Viti Levu, with 64 and 68 ins. respectively, and Richmond on Kadavu with 67 ins. The mean annual rainfall for localities in the Lau Group is between 70 and 80 ins. There is a very definite seasonal change in rainfall in all parts of Fiji, and this is of great importance in connection with *P. reichei*. The seasonal variation and the variation in total rainfall are sufficiently exemplified in Table I below.

*Table I. Average Rainfall in Different Parts of Fiji.*

| Locality, and Island or Group. | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. | Total for Year. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. Lakeba, Lau | 10·12 | 6·78 | 10·12 | 8·73 | 7·22 | 2·96 | 4·55 | 5·32 | 3·44 | 6·45 | 8·36 | 4·86 | 78·91 |
| 2. Munia, Lau | 7·85 | 7·62 | 8·88 | 8·12 | 5·77 | 4·15 | 2·79 | 3·96 | 3·42 | 4·99 | 5·71 | 6·84 | 70·08 |
| 3. Nabavatu, Lau | 7·91 | 8·26 | 11·03 | 9·84 | 6·54 | 4·53 | 2·83 | 3·85 | 3·64 | 4·46 | 5·37 | 7·45 | 75·71 |
| 4. Lautoka, Viti Levu | 8·95 | 12·33 | 12·06 | 5·86 | 4·38 | 2·18 | 2·04 | 3·51 | 2·07 | 3·40 | 4·16 | 7·37 | 68·31 |
| 5. Nausori, Viti Levu | 12·25 | 12·43 | 14·18 | 12·07 | 9·92 | 6·38 | 4·48 | 6·62 | 6·64 | 7·68 | 8·81 | 13·05 | 114·51 |
| 6. Suva, Viti Levu | 11·41 | 10·70 | 14·50 | 12·20 | 10·08 | 6·69 | 4·93 | 8·29 | 7 67 | 8·28 | 9·79 | 12·51 | 117·05 |
| 7. Labasa, Vanua Levu | 13·03 | 14·20 | 13·92 | 8·68 | 4·49 | 2·27 | 1·87 | 1·70 | 2·27 | 3·32 | 5·37 | 9·92 | 81·49 |
| 8. Nabouwalu, Vanua Levu | 11·98 | 13·17 | 12·92 | 12·28 | 8·73 | 4·97 | 4·03 | 4·70 | 5·54 | 6·28 | 8·35 | 12·77 | 105·84 |
| 9. Savu Savu, Vanua Levu | 11·57 | 10·07 | 12·23 | 9·87 | 8·35 | 5·28 | 4·75 | 6·30 | 6·88 | 7·66 | 8·06 | 11·77 | 102·78 |
| 10. Waiunu, Vanua Levu | 18·28 | 17·77 | 18·16 | 15·38 | 11·40 | 6·43 | 5·67 | 6·94 | 9·16 | 10·88 | 12·08 | 16·38 | 148·54 |
| 11. Vuna, Taveuni | 12·60 | 13·23 | 10·46 | 13·81 | 8·90 | 6·04 | 6·15 | 7·30 | 8·94 | 9·17 | 8·16 | 12·12 | 116·89 |
| 12. Salialevu, Taveuni | 14·81 | 17·10 | 14·11 | 18·59 | 19·66 | 16·25 | 13·78 | 14·05 | 28·25 | 20·89 | 15·55 | 20·16 | 213·20 |
| 13. Waiyevo, Taveuni | 11·27 | 12·47 | 12·02 | 9·54 | 8·81 | 5·31 | 2·35 | 3·61 | 5·21 | 7·46 | 9·69 | 11·22 | 98·96 |
| 14. Levuka, Lomaiviti | 9·32 | 10·51 | 12·03 | 10·39 | 7·04 | 4·52 | 3·70 | 5·45 | 5·32 | 5·59 | 8·11 | 9·08 | 91·08 |
| 15. Makogai, Lomaiviti | 7·23 | 6·96 | 10·94 | 10·18 | 6·86 | 3·88 | 3·24 | 3·93 | 4·10 | 4·31 | 6·01 | 10·72 | 78·36 |
| 16. Richmond, Kadavu | 7·44 | 8·73 | 7·00 | 5·96 | 7·32 | 3·74 | 3·43 | 6·04 | 3·88 | 5·20 | 3·53 | 5·22 | 67·46 |
| 17. Rabi | 16·58 | 16·37 | 17·43 | 17·15 | 13·69 | 7·45 | 4·65 | 6·41 | 7·70 | 8·70 | 11·32 | 16·34 | 149·79 |

## E. Description of Stages.

1. **Egg.** (Figs. 1 and 2 and Plate I.)

The egg is entirely hidden beneath an opaque capsule, and is therefore normally invisible. Its ventral surface is in close contact with the leaf, and the capsule covers the dorsal surface and is in contact all round its edge with the leaf and all over its inner surface with the egg. The capsule is strongly convex and broadly oval in outline. The outline of the anterior end is a semi-circle and that of the posterior end a parabola. The colour is pale straw. The capsule consists of numerous, semi-digested, fragments of coconut-leaf tissue, irregularly arranged and strongly stuck together. Its inner surface is smooth and shiny on

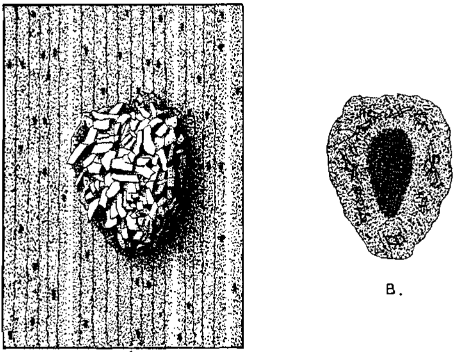



Fig. 1.—*Promecotheca reichei.* A, typical egg capsule on underside of coconut leaflet ( × 12) (cf. Plate VI, a, for natural size). B, typical egg capsule removed from leaflet and reversed, showing flat under surface and egg in situ ( × 12).

account of close contact with the egg, to which it adheres firmly, but its exposed surface is jagged because the leaf fragments project in a wholly haphazard manner. The rim of the capsule and the ventral surface of tbe egg adhere firmly to the leaf, and together form a plane surface. The binding substance which holds the leaf fragments together is strong and tough, and round the edge of the capsule it extends slightly over the leaf surface to form a thin, transparent, flange. The capsule, and the contained egg, can be removed from the leaf and turned over without damage by the insertion of a needle beneath the flange, and the flange is then seen as a broad frame round the egg.

The egg itself resembles a duck's egg in outline, and it is translucent and golden-brown in colour. Its surface is perfectly smooth. Ventrally

it is flat and dorsally convex, and it is highest at about one-third of its length from the anterior (broader) end. The chorion is flimsy, pliable, transparent, and easily fractured. It is possible to dissect away the capsule, bit by bit, without breaking the egg; but this is a difficult operation, and the best method of obtaining eggs without capsules for observation purposes is to find beetles which are about to oviposit and then disturb them before they have time to construct the capsules.

The mean length of the capsule is 2·40 mm., and that of the egg is 1·52 mm. The mean height of the egg is 0·34 mm.

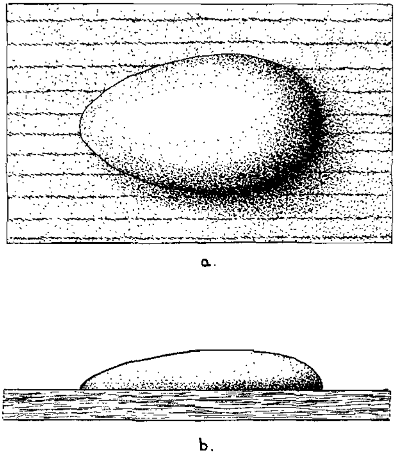


FIG. 2.—*P. reichei.* Egg without capsule; a, dorsal; b, right lateral (× 30).

2. **Larva.**

There are three larval instars. The external morphology of the larva is practically the same in all instars, and it is convenient, therefore, to describe the full-grown larva first and then to point out the few differences that exist in the earlier instars.

a. *3rd Instar* (Plates I and III). The larva is elongate and considerably flattened, its form being typical of leaf-miners in general. It is broadest across the 2nd segment and narrows regularly from that segment to the posterior extremity. The head is almost completely enclosed by the 1st segment, so that only the mouth-parts protrude. There are 13 segments, and the segmentation is very marked. All the segments except the 1st are of similar form.

The 1st segment (the prothorax) is very large and approximately triangular in outline. It consists of two similar, strongly chitinised, plates, one dorsal and one ventral, which are hard but pliable, and these are *joined together on either side by a fleshy fold of soft skin.* Each plate is slightly wrinkled transversely, and anteriorly is strongly reticulated and much more heavily chitinised. The reticulated area borders the opening through which the anterior end of the head protrudes. The reticulations have the appearance of tiles, each sloping upwards posteriorly so that it is higher than the anterior edge of the one behind it. The colour of this segment is a rich brown, except for the fleshy lateral folds which are yellow, and the plates are very shiny.

All the other segments are soft, non-chitinised, and bright yellow, so that the larva as a whole appears yellow and fleshy. The 2nd and 3rd segments (the meso- and meta-thorax) are smoothly rounded laterally, but each of the remaining segments (the abdominal) except the last bears on each side a large, fleshy, non-chitinised, tubercle. Each of these tubercles is seen, when the larva is viewed from the side, to be ovoid in shape and to be orientated diagonally so that its anterior end is below and in front of its posterior end. Each tubercle bears about 6 short hairs, distributed over its surface. Above each tubercle, and just above and slightly behind each spiracle, there is another small group of hairs (usually 4).

The first three segments (the thoracic) bear no tubercles; but they bear lateral hairs corresponding to, but more numerous than, those on the abdominal segments.

There is a row of minute chitinised teeth along the posterior, dorsal, border of the 11th segment, but except for these and the hairs already mentioned, the body is entirely naked and devoid of appendages of any kind.

There is a slight transverse furrow across each abdominal segment, both dorsally and ventrally, and each furrow is narrow at the centre and widens out at each end. On the 2nd and 3rd segments, dorsally and ventrally, only the ends of the furrows are present; and just behind each end of the ventral furrow on each of these two segments there is a very small, oval, slightly depressed area. The skin in these shallow depressions bears several extremely minute setae, but is not reticulated, and in this latter respect it differs from that of all other parts of the body. A corresponding and similar depression is present ventrally near each posterior corner of the prothorax. It seems probable that these 6 depressions mark the positions of the lost thoracic appendages, and are, in fact, vestiges. In this connection it is noteworthy that in one remarkable larva, which moulted three times instead of the usual two, each of the three thoracic segments in the last (4th) instar bore a pair of appendages at these points, each appendage being in the form of an elongate lobe, terminally rounded.

The skin is very minutely reticulated all over the body. There are 9 pairs of spiracles, situated laterally. The first pair is on the 2nd segment and the others are on segments 4 to 11 inclusive.

The dorsal and ventral aspects of the body are very similar, but are nevertheless readily distinguishable by the last segment, which

bears the anus and is almost wholly ventral. Moreover, the back is slightly arched longitudinally.

The mean length of the larva, when full grown and not abnormally extended, is 9·5 mm., and the mean width of the prothorax is 2·2 mm.

The larva has already been described and figured by Maulik.*

He described it from a single specimen mounted as a microscope preparation, and evidently the larva described was not in the last instar, since it is stated to measure about 4 mm. only when fully extended after *potash treatment*; but the description, though incomplete, is accurate in most respects. Reference is made, however, to a "series of triangular structures visible between the last two abdominal segments, appearing to lie between the dorsal and ventral surfaces of the body." These are presumably the chitinous teeth on the posterior, dorsal, border of the 11th segment, and the fact that they appeared, in the specimen as mounted, to lie within the body is attributable to accidental folding of the skin in that region.

The head is described by Maulik, and no further account of it is necessary here since his description applies to the full-grown larva also.

b. 1*st and* 2*nd Instars* (Plates I and II). The external morphology in the two earlier instars is almost identical with that already described for the 3rd instar. The hairs are slightly longer, relatively to the dimensions of the body, in the earlier instars. The chitinous teeth on the 11th segment are present in all instars. The dimensions of the prothorax, however, are an infallible means of recognising the different instars. The mean width of the prothorax in the 1st instar is 1·09 mm. and in the 2nd instar 1·50 mm. Since the protborax is strongly chitinised almost to its margin, its width remains nearly constant throughout each instar. The length of the 1st-instar larva increases from 1·7 mm., when it is newly hatched, to 2·9 mm., when it ceases feeding prior to the first moult.

The prothorax of the newly-hatched larva is relatively enormous, the rest of the body, prior to the commencement of feeding, being in a *completely contracted condition*.

3. **Pupa.** (Plates I and III.)

The pupa is golden-brown in colour throughout, and without markings. Its mean length is 7·8 mm. Its surface is shiny, but greatly furrowed and indented. The sheaths of the appendages are closely apposed to the body. The abdomen consists of 9 segments. All the abdominal segments, except the last which is ventral and incapable of separate movement, are articulated for movement, and are separately visible dorsally. The first three abdominal segments are invisible ventrally, being covered by the leg- and wing-sheaths. On the dorsal surface of the prothorax there is a median longitudinal furrow, and on the mesothorax, dorsally, there is a pair of large depressions. The metathorax has a median, longitudinal, ridge, dorsally, which widens anteriorly to enclose a pear-shaped depression. The prothorax and the metathorax each have a prominent ridge along their posterior dorsal

* Maulik, S. 1929. Insects of Samoa. Pt. IV, fasc. 3, p. 211.

margins. There are a few scattered hairs on the thorax, particularly on the sides of the prothorax. The abdomen bears 7 pairs of spiracles (on its first 7 segments). On each abdominal segment there is a mid-dorsal pair of short, stout, spines, and outside these, on either side, there is a similar subdorsal spine. There is a transverse ridge across each abdominal segment, near its posterior margin, and on this ridge there is a series of minute spines, variable in number. Every one of the spines bears at its base a minute seta. On either side of each abdominal segment there is a small group of minute spines, each bearing a seta which is considerably longer than any of the dorsal setae. There are no spines on the ventral surface, but ventrally the first 4 exposed segments are ridged medially and longitudinally. The body terminates posteriorly in a transverse row of 10 short, stout, spines situated on a backwardly-directed ridge which forms the posterior border of the 8th abdominal segment and overhangs the small 9th segment.

4 **Adult.** (Plates I, II, and IV.)

The adult was first described in 1869 by Baly (*Trans. Ent. Soc. Lond.*, 1869, p. 374), in the following terms :—

> "Angustata, subcylindrica flava, intida, tarsis pallide piceis, *abdomine, mandibulis, oculis antennisque (harum articulo basali* excepto) nigris; elytris fortiter punctato-striatis, metallico-caeruleis, tertia parte antica flava.
>
> Long. $3\frac{1}{2}$–$4\frac{1}{2}$ lin.
> Hab.—Vavao.
>
> Antennae two-thirds the length of the body in the ♂, rather *shorter in the* ♀, *slender, filiform, black, the basal joint flavous,* the second and third, in the ♂, pale piceous. Thorax much longer than broad, moderately constricted at the base, sides slightly but distinctly swollen in front of the constriction; surface smooth and shining, impunctate. Elytra parallel, regularly rounded at the apex, their anterior third flavous, the remaining portion metallic blue."

The sexual dimorphism is not marked, but the sexes can nevertheless be distinguished with certainty, even when the beetles are alive, by the following characters (which are illustrated in the plates) :—(*a*) In general, males are smaller than females, but large males are the same size as small females. (*b*) In the males, the elytra (when closed) are almost parallel-sided and are not wider posteriorly than anteriorly; in the female, the elytra widen slightly posteriorly. (*c*) The abdomen of the male is much narrower, relative to its length, than that of the female; this is particularly noticeable when the insects are viewed ventrally (Plate II, d). (*d*) The abdomen of the male, as seen from below, is much less hairy at its extremity than that of the female; this difference is readily observed because the hairs glisten in the light, and it is due to the presence in the female of tufts of hairs on the external genitalia which project from beneath the 5th visible abdominal sternite.

The digestive system (fig. 3, A) is comparatively simple. There are no salivary or pygidial glands, and there is no gizzard. The crop is large, and it tapers posteriorly to merge with the mid-gut, there being no definite point of separation. The hind-gut is clearly divided into ileum, colon, and rectum. The malpighian tubes are long and are always six in number. At the extreme anterior end of the crop, there are 4 small vesicles, presumably glandular, and each opens separately into the crop via a very short duct.

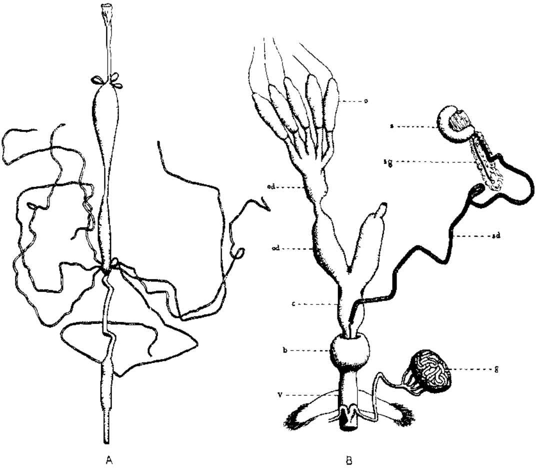



FIG. 3.—*P. reichei*: internal anatomy. A, digestive system (for explanation see text). B, reproductive system of newly-emerged female, dorsal view, showing immature ovary (right ovary and left colleterial gland removed): b, bursa copulatrix; c, common oviduct; g, colleterial gland; o, ovariole; od, left oviduct; s, spermatheca; sd, spermathecal duct; sg, spermathecal gland; v, vagina.

The female reproductive system is illustrated in figs. 3 and 4. There are 5 ovarioles in each ovary, and in immature females these lie in one plane so as to resemble the fingers of a hand. Their filaments unite distally. The oviduct of each side is a very broad tube, with a constriction near its centre. The common oviduct is very short; it is broad anteriorly but it narrows posteriorly and is normally somewhat telescoped into the vagina, the anterior end of which is large and is dorsally swollen to form the bursa copulatrix. The spermatheca, which is strongly chitinised, is curved in a semi-circle. It bears at its distal

end a short process for the attachment of muscle, and near its proximal end there is a small rounded projection at the apex of which the duct of an elongate gland opens. This gland surrounds its duct throughout its length, and the duct has a globular swelling at its point of origin in the distal end of the gland. The distal process and the proximal projection on the spermatheca are very strongly chitinised. The spermathecal duct, which is also strongly chitinised, is very long and tightly coiled; at its proximal end it opens into the vagina dorsally, beneath the overlapping bursa, and at its distal end it opens into the spermatheca at the base of the projection into which the gland opens. There is a pair of comparatively large colleterial glands associated with the vagina. Each of these is ovoid and compact, and its surface, when suitably stained, shows brain-like convolutions; arising from it are 5 short ducts which unite to form a single, rather long, duct, and this joins its fellow of the other side to form a very short common duct which opens into the vagina dorsally. The opening of the common duct is extremely close to the external opening of the vagina. The duct of each side is swollen and recurved at the point of junction with the common duct, and the swollen portion, which is thick-walled and rigid, forms with its fellow a bilobed projection from the vagina. There is little doubt that these glands secrete the fluid which is deposited on the eggs after they are laid and which cements together the fragments of leaf to form the egg-capsules.

At the time when the female emerges from the mine, the ovaries are very small and no oocytes are yet differentiated, but as the oocytes develop the ovaries increase enormously in size, since the mature eggs are very large. The great increase in size can be judged by comparing the ovaries with the spermatheca in figs. 3 and 4. Each egg, when mature, passes into the oviduct and completely fills it, so that there are never more than 2 mature eggs (one in each oviduct) in one beetle at the same time, and no beetles can lay more than 2 eggs per day. In each ovariole 2 eggs, one much further developed than the other, are present at the same time, and it seems probable, judging from observations of the total number of eggs laid, that the maximum number of eggs which one ovariole can produce does not exceed 3.

The male reproductive system (fig. 4) is of simple form. The testes are large, compact, ovoid bodies, constricted medially. The constriction divides each testis into two equal parts which are nearly spherical, and each part is a single follicle. Each follicle appears to consist of 7 (occasionally 8 or 9) segments arranged radially, but this appearance is superficial only, being due to strands of connective tissue tightly stretched round the follicle. A duct (vas eferens) arises from the centre of each of the two follicles, and the two ducts unite to form the vas deferens. The latter is short. Near its middle point there is a minute, ovoid, swelling, and from this a rather larger, ovoid, vesicle arises; the two together resemble a cottage loaf in shape and presumably constitute the vesicula seminalis. There are no accessory glands. The two vasa deferentia unite to form a thick-walled duct whose length is nearly twice that of either of them, and this duct is continuous posteriorly with the much narrower ejaculatory duct. The latter is extremely

long, and when straightened out it measures approximately 40 mm. and is nearly 6 times the length of the beetle which contains it. The *ejaculatory duct terminates in the large and strongly* chitinised oedeagus,

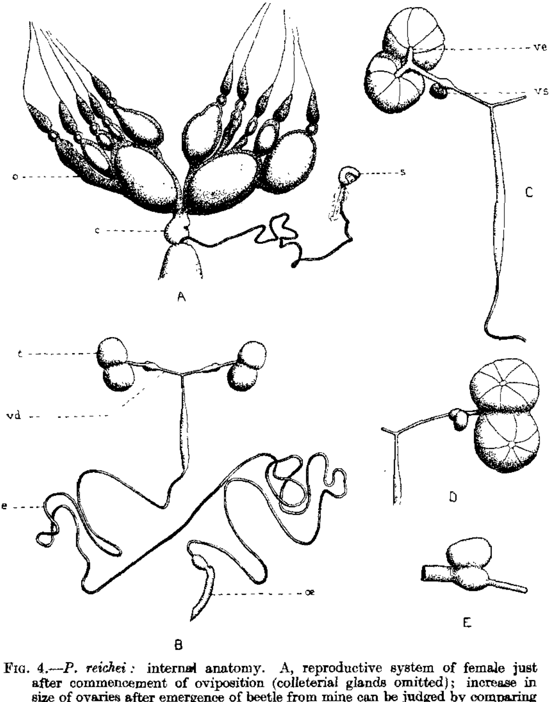



FIG. 4.—*P. reichei:* internal anatomy. A, reproductive system of female just after commencement of oviposition (colleterial glands omitted); increase in size of ovaries after emergence of beetle from mine can be judged by comparing fig. 3, B, in which the magnification is much greater as indicated by the spermatheca, the size of which is constant. B, male reproductive system. C and D, dorsal and ventral aspects of testis and vesicula seminalis. E, vesicula seminalis; e, ejaculatory duct; oe, oedeagus; t, testis; vd, vas deferens; ve, vas eferens; vs, vesicula seminalis.

which is of the usual form for Coleoptera. The wall of the lumen of the ejaculatory duct is very strongly chitinised throughout its length.

The thick-walled common duct, the vesicula seminalis, and that part of the vas deferens which lies between them, appear also to be lined internally with chitin, though the chitinous lining is here very thin as compared with that of the ejaculatory duct. The chitin is, in fact, continuous from the seminal vesicle to the oedeagus. In specimens treated with potash, the testis, the larger portion of the seminal vesicle, and that part of the vas deferens which lies between them, disappear completely, but the smaller portion of the vesicle, the remainder of the vas deferens, and the common duct, persist and remain rigid. This is noteworthy because only the ejaculatory duct, presumably, is of ectodermal origin.

## F. Life History.

### 1. Egg.

The eggs are almost invariably laid on the undersides of the leaflets of the coconut palm. Very rarely one is found on the upperside of a leaflet, but this only occurs when the beetles are excessively abundant. Unlike those of certain other species of *Promecotheca*, the eggs of *P. reichei* are not sunk into the leaf tissues, but are wholly on the surface. There is only one egg in each capsule, and in this respect also *P. reichei* differs from certain other species. The capsules are conspicuous objects on the leaves, on account of their comparatively large size, light colour, and convexity. The egg is normally situated nearer the base than the tip of the leaflet and is normally orientated so that its long axis is parallel to the mid-rib and "veins" of the leaflet and so that its anterior end is directed towards the distal end of the leaflet. The ventral surface of the egg is that which is in contact with the leaflet. The orientation of the egg is of importance in connection with the mining habits of the resulting larva. When the beetles are very abundant, but never in any other circumstances, a few eggs are laid near the tips of the leaflets; and the majority of these are orientated so that their anterior ends are directed, not towards the tips as is normally the case, but towards the bases of the leaflets. Consequently, no matter in what part of the leaflet an egg is situated, the resulting larva has, in front of it, plenty of leaf tissue in which to mine.

The adhesion of the capsule to the leaflet is very strong and lasting, and in dry weather nearly all the capsules remain on the leaflets for at least 3 months, and the majority for 6 months or longer. Consequently capsules of more than one generation are to be seen together on the leaflets of the older leaves. In wet weather, the capsules become softened and are then easily displaced, but in all circumstances they remain on the leaflets long after the contained eggs have hatched.

### 2. 1st-Instar Larva.

The embryo develops in a straight position in the egg (fig. 5), and therefore when the egg hatches the larva begins mining towards the tip of the leaflet, except when the egg is situated near the tip. The larva effects its exit from the egg and its entry into the leaf in one operation, so that the curved slit by which it enters the leaf is permanently

covered by the egg-capsule. On account of this method of hatching, the width of every mine at its commencement is approximately equal *to the width of the egg, and since the egg is laid with its ventral surface* in contact with the lower epidermis of the leaf, every larva is orientated within its mine so that its ventral surface is in contact with the upper epidermis. Being unable to turn over in the mine because of its flatness, it retains this orientation throughout its life. The commencement of a mine is illustrated in fig. 6.

The larva always mines in a direction parallel to the veins of the leaflet, unless forced by dead tissue to turn aside. All mines in normally

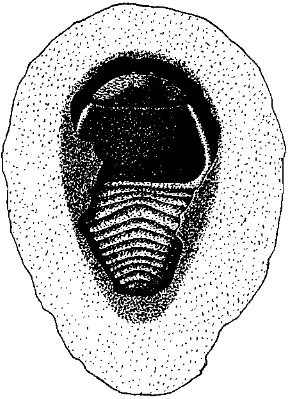
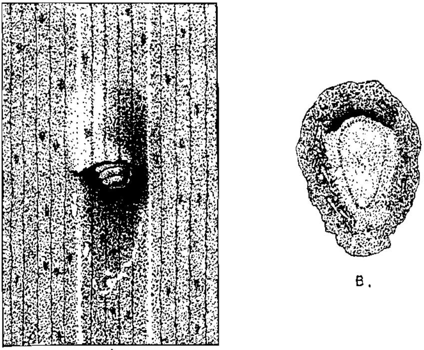


FIG. 5.—*P. reichei.* Egg, in capsule, removed from leaflet and turned over, with part of chorion removed ventrally to show contained larva just before hatching (× 33). (Slightly diagrammatic.)

healthy leaflets are therefore straight and very much alike in shape and size, and all in one leaflet are parallel. A typical 1st-instar mine when completed is 25–30 mm. long; and at one end its width is equal to that of the egg and at the other end is 4–5 mm. The width normally increases regularly from the egg-capsule to about the middle point of the mine, but from that point onwards the width is usually constant, the mine being bounded by leaf veins which are parallel. In abnormally tough leaves, however, particularly in dry weather, the mines are often greatly attenuated and may attain a length of 52 mm. The width of such mines is approximately constant at about 1·3 mm. Their abnormal length and narrowness are due to abnormal toughness of the veins in the leaves, the larva being unable to bite through them. Another frequent result of dry weather is that the leaf tissues just in front of the

mine dry and die before the larva has time to devour them, and it then turns aside and bites, if it can, through a vein to reach new tissue, so that the mine acquires a sharp kink. Very often in these circumstances the larva dies of starvation, being unable to bite through the veins which bound its mine at the sides or through the dry tissues at the end of it. This applies, however, only to 1st-instar larvae. Larger larvae feed much more rapidly, and even in dry weather the tissue in front of their mines does not dry before they can devour it.

As it feeds, the larva moves slowly from side to side within the mine in such a way as to cause the end of the mine to assume a roughly semicircular outline. It excretes at frequent intervals, and its constant



A. B.

FIG. 6.—*P. reichei.* A, commencement of mine as seen on underside of leaflet after removal of capsule; posterior extremity of larva (normally covered by capsule) projecting from mine, larva not yet having penetrated completely into leaf tissues; former position of capsule indicated vaguely by white spots due to discoloration resulting from contact ($\times$ 12). B, capsule, after hatching of egg, turned over to show curved slit in chorion (corresponding to slit in leaflet) through which larva escaped ($\times$ 12).

movement from side to side causes the excrement to accumulate chiefly at the sides of the mine. The excrement, even when first deposited, is only slightly moist, and very soon it becomes quite dry and breaks up to form a powder. The mine is therefore lined, all along each side, by a tightly-packed, powdery, brown mass, but is empty in the centre, except for scattered fragments of excrement.

The larva feeds almost continuously at the end of the mine until it is ready to moult, but its growth is very slow for a tropical insect. When it has attained the maximum size for the 1st instar it withdraws from the end of the mine and takes up a position near the other end, close to the egg-capsule. It then undergoes a lengthy resting period, in this

position, prior to the first moult. During this period it acquires a characteristic appearance, becoming much paler in colour and very tightly distended.

The mine itself changes in appearance during the resting period. So long as the larva is feeding, the growing end of the mine is green, and owing to the removal of the central tissues the leaflet is semi-transparent at this point and the larva can be seen vaguely through either epidermis when the leaflet is held up to the light. The upper and lower layers of epidermis do not normally die until about 2 days after the larva has removed the intervening tissue. When dead, they are brown and quite opaque; and consequently the mines, even of the 1st instar, are conspicuous on the leaves as elongate, brown, scars, sharply outlined against the surrounding, undamaged, green tissues. The green of the growing end of each mine merges into the brown, and the green end, as seen on the upper surface of the leaf, is as sharply outlined as the larger brown portion of the mine because its green colour is much lighter than that of the surrounding healthy tissues, the larva having almost completely removed the green tissue in contact with the inner surface of the upper epidermis. As seen on the lower surface, on the other hand, the growing end of the mine is never clearly outlined, and except when held up to the light is indistinguishable from the surrounding tissues, because the larva does not mine so close to the lower epidermis as to the upper so that a layer of green tissue remains attached to the lower epidermis. This difference in appearance between the upper and lower surfaces of the mine while the larva is feeding is equally apparent in the two later instars, since the larva feeds in precisely the same manner in all instars. When the larva ceases to feed, however, prior to moulting or because it is parasitised, the mine, on both surfaces of the leaf, becomes brown all over and clearly outlined all round its edge.

The presence of the larva causes the thin upper wall of the mine to stretch and bulge slightly, so as to acquire a permanent transverse convexity. The lower wall, being much thicker, does not bulge.

Typical 1st-instar mines are illustrated in Plate VI, a.

### 3. 2nd-Instar Larva.

The larva moults in the mine in the position to which it withdraws when it ceases to feed. Consequently, the cast skin of the 1st instar is always to be found near the narrow end of the mine. The skin of the head, which is cast separately, and that of the prothorax, to which the skin of the other body segments remains attached in a greatly shrivelled condition, are conspicuous in the mine because, being strongly chitinised, they do not shrivel. At the time of moulting, and for a few hours subsequently, the head and prothorax of the larva are soft, and pale in colour, like the rest of the body, but they gradually harden and become brown. During the hardening process, the larva still remains motionless in the same position at the narrower end of the mine, but when this process is completed, it advances once more to the other end and recommences to feed where it ceased feeding prior to moulting. During the resting and moulting period the boundary tissue at the end of the

mine dies and dries in a hard line, dark brown in colour, and the larva has first to penetrate this line of hard tissue. As soon as it has done so, it has healthy green tissue in front of it again, and on this it feeds in exactly the same manner as before, only much more rapidly now on account of its larger size. The beginning of the 2nd-instar mine is apparent, on the upperside of the leaf, as a small, light green, band along the wider end of the now completely brown 1st-instar mine. The larva continues mining in the same direction as before, and as it penetrates further and further along the leaflet, the epidermal tissue behind it turns brown like that of the 1st-instar mine; but the dark line which marks the end of the latter persists permanently, so that it is always possible, even in very old mines, to see the limit of the 1st-instar section on both sides of the leaflet, though the line is more clearly apparent on the lower than on the upper surface.

The beginning of the 2nd-instar mine is the same width as the end of the 1st instar, but the larva, as it advances, steadily widens the mine until it attains a width of 8·0 mm. on the average (the actual width attained varying from 7·0 mm. to 11·0 mm.). Having widened the mine to this extent, the larva maintains approximately the same width throughout the remainder of the instar, with the result that the distal part of the 2nd-instar mine is roughly parallel-sided like that of the 1st instar, but is approximately twice the width of the latter. The length of the 2nd-instar section of the mine, when completed, varies from 24 to 48 mm., the mean being 31 mm., and therefore the mean total length of the mine at this stage, as measured from the egg-capsule, is approximately 58 mm. *These measurements are typical for all mines in normally* healthy leaves, but if the leaves are abnormally dry, great attenuation of the 2nd-instar mines results, as in the case of the 1st instar, and if the growing ends meet other mines, or feeding scars of other insects, extensive distortion occurs.

Having attained its maximum growth for the 2nd instar, the larva once again withdraws from the end of the mine to prepare for moulting. It does not withdraw to the same position as before, however, but only as far as the end of the 1st-instar section of the mine. It again becomes tightly distended and much paler in colour, and the mine becomes brown at its extremity as elsewhere.

Typical 2nd-instar mines are illustrated in Plate VI, b.

### 4. **3rd-Instar Larva.**

The second moult, which brings the larva to the last instar, is precisely the same as the first, except as regards the position of the larva in the mine. The cast skin is left, on this occasion, near the end of the 1st-instar section of the mine. The larva resumes feeding in the same manner as before, and a dark line, due to the hardening of the tissues across the end of tbe mine during the moulting period, marks the limit of the 2nd-instar section of the mine and is similar to the line which terminates the 1st-instar section. Thus, every mature mine is superficially divided into 3 sections, and each section represents the extent of feeding in one instar. The two transverse lines are very useful as a means of ascertaining the stage of larvae in the field without opening

the mines, but it must be borne in mind that occasionally a third line appears as a result of an abnormal third moult or as a result of the temporary cessation of feeding when water enters the mine.*

Since the 3rd-instar larva is large, the mine now grows comparatively rapidly and becomes very conspicuous on the leaf. When viewed from the ground against a bright sky it appears as a long black scar, but when viewed against a dark background its actual colour is seen to be light brown. The bulging of the upper wall of the mine, already noted in connection with the 1st instar, is very pronounced in the 3rd instar and persists throughout the later stages; and throughout the larval life the excrement is deposited mainly along the sides of the mine, though not at the extreme edges, in the manner already described. When a 3rd-instar mine, in which the larva is still feeding, is held up to the light, the larva is very plainly visible in silhouette through the green tissue at the end of the mine; and the excrement, and the superficial veins and cross-veins which lie in the walls of the mine are also apparent. Four typical mines, viewed in this way, are shown in Plate VII, a.

When the large mines are abundant, it frequently happens that a larva meets the hard line of tissue which borders another mine. A 3rd-instar larva is quite capable of biting through this hard tissue and entering the other mine, but it never does so, and therefore there is never more than one larva in one mine; instead it always withdraws and bites through the hard tissue which borders its own mine, so that a branch mine is formed. It may even turn round and begin feeding at the narrow end of its mine where the egg-capsule is situated, thus extending the mine in the opposite direction and widening the ordinarily narrow end of it so that eventually the mine is equally wide at both ends and has in its centre a much narrower portion representing the end of the 1st instar and the beginning of the 2nd instar. In fact, mines of every conceivable shape occur when many are present in every leaflet. In all other circumstances, however, the mine is approximately straight, beginning nearer the base of the leaflet and extending towards the tip of it, and this must be regarded as the typical form.

Although it normally moves very little, the larva, in all instars, is capable of very energetic and rapid movement in both directions in the mine. If removed from the mine, however, it is absolutely helpless, and it is entirely incapable of re-entering a leaf. Within the mine, it moves backwards as readily as forwards, and in no circumstances does it turn round so as to face in the opposite direction except when it requires to feed at the narrower end because the broad end is obstructed. The only occasions when it moves rapidly are when it feels the attack of a natural enemy or pressure from the outside of the mine. Its movement along the mine, backwards or forwards, is effected by a series of wave-like contractions and expansions of successive segments. It is in contact, above and below, with the walls of the mine, and its movement is facilitated by its lateral hairs and by the row of chitinous teeth on the 11th segment. These chitinous teeth, however, are in no way essential for movement, as the larva can progress in either direction as rapidly when it is placed between two sheets of glass as it can in its mine, and

* These phenomena are discussed later (p. 36).

the teeth do not grip the glass. Nevertheless, they have an important function. They serve to enable the larva to grip the lower wall of the mine with exceptional firmness while it is thrusting its head into the end of the mine to feed. The upper and lower epidermal layers of the leaflet are necessarily very close together at the ends and edges of the mine, and the distance between them is very much less than the normal thickness of the head of the larva when it is not subjected to pressure. Consequently, a firm grip and exceptional force are necessary before the mouth-parts can reach the extreme edge of the mine.

The width of the typical mine is not greatly increased after the 2nd instar; and often it is not increased at all, the 3rd-instar section being confined between the same two veins as the later part of the 2nd-instar section. If there is any increase it usually takes place over a short distance only at the very beginning of the 3rd instar. Consequently, the whole or almost the whole, of the 3rd-instar section is typically parallel-sided. The extremity of a mature mine (*i.e.* a mine in which the larva has finished feeding) is roughly semi-circular. The mean width of typical 3rd-instar portions of mines is 10 mm. (the variation being 8 to 13 mm.), and their mean length is 97 mm. (the variation being 82 to 130 mm.).

Typical mature mines, which have suffered no abnormal distortion or attenuation, have a mean total length, as measured from their egg-capsules, of 150 mm., but the length varies from 130 to 180 mm. Exceptionally attenuated mines, however, attain a maximum length of no less than 230 mm. (9 inches).

The larva withdraws backwards from the end of the mine when it is fully fed, and takes up a position in, or just in front of, the 2nd-instar section. This withdrawal is the commencement of the prepupal condition.

Typical mature mines are illustrated in Plates VIII and IX.

### 5. Occasional Occurrence of a Fourth Larval Instar.

Very rarely larvae moult three times, so that there are 4 larval instars in such cases. No reason for this was ever discovered, and the larvae concerned produce normal adults, of both sexes. Since, at the same time, all the neighbouring larvae in the same leaves and leaflets moult the usual three times, the abnormal fourth moult is not attributable to climatic factors or to any factors inherent in the trees themselves. The extra moult causes a third transverse line to appear on the mine, but this line is liable to be confused with the additional one that results from the entry of water into the mine. The number of lines, therefore, is not a conclusive test for the number of moults, but if a 4th instar occurs, the three cast skins are readily visible within the mine, and this is the final test.

### 6. The Tissues devoured by the Larva.

The arrangement of the various tissue layers and of the three series of veins (vascular bundles) in a coconut leaflet is illustrated in fig. 7.

Green parenchymatous tissue, in which the cells are very closely

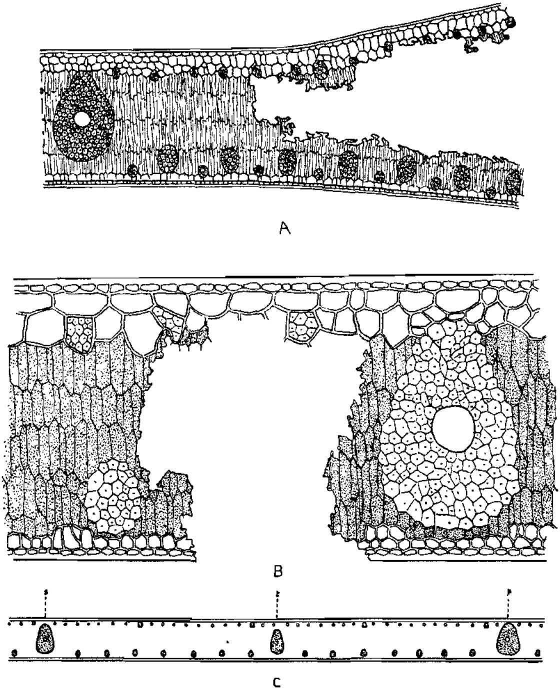



FIG. 7.—A, transverse section through coconut leaflet freshly mined by larva of *P. reichei* (only half of the mined portion is shown), to illustrate nature of mine relative to tissue layers of leaflet. B, transverse section through coconut leaflet freshly attacked by adult *P. reichei*, to show nature of damage to tissues. C, diagrammatic transverse section through coconut leaflet, to show arrangement of veins and veinlets (p, primary vein; s, secondary vein; t, tertiary vein).

(For further explanation of A, B, and C, see text.)

packed, occupies the whole of the space between the two colourless epidermal layers. The veinlets of the upper surface lie almost wholly outside the green tissue, but those of the lower surface are almost completely within it.

The food of the larva consists solely of green tissue, except for the few primary, secondary, or tertiary veins which it requires to bite through in order to widen its mine as it grows. It has considerable difficulty in biting through these veins from the side, and therefore as soon as it has sufficient room to permit free movement it ceases to widen the mine. From this time onwards the vein on each side of the mine is a partial obstruction which the larva has no need to overcome, and consequently the rest of the mine is normally parallel-sided. The veinlets near the lower epidermis, being very close together, prevent it from eating the green tissue which lies between them, but without penetrating this layer, it has ample green tissue in front of it. It is the presence of these veinlets along the lower epidermis which causes the lower wall of the mine, as we have already noted, to be thick and the growing end of the mine, as seen on the lower surface of the leaflet, to be green and indistinguishable from the surrounding undamaged tissue. The veinlets near the upper surface, on the other hand, do not project appreciably into the green tissne; and consequently the larva leaves only the colourless tissue to form the upper wall of the mine, and the growing end, as seen on the upper surface of the leaflet, is sharply outlined against the green of the surrounding undamaged tissue. Actually, a few fragments of green parenchyma are left here and there along the veinlets and cross-veins of the upper wall (fig. 7, A), and it is these which give the light green colour to the upper wall at the growing end of the mine, although it consists very largely of colourless tissue.

Since the larva ean feed much closer to the upper epidermis than the lower, the upper wall of the mine is always very much thinner. The adult beetles, and all the parasites, almost invariably emerge through the upper wall for this reason.

The cells of the two epidermal layers become dry a few days after the larva has passed them, and the walls of the mine are then light brown and opaque. The thin upper wall is very flexible, like paper, and it tears in strips longitudinally on account of the parallel veinlets in it. The lower wall is comparatively rigid and tough, and it does not tear easily or in straight lines because of the presence of thick cross-veins.

The mines change in colour from brown to grey in the course of time, and finally become almost white, but no appreciable change occurs until long after the beetles have emerged. The cells between the veinlets in the walls gradually crumble away, until only the veinlets and the single outer layer of epidermal cells, together with the cuticle, remain. In this condition, the walls are remarkably resistant to the action of wind and rain, and they remain intact for many months and often until after the leaves in which the mines are situated have dropped to the ground. Strong gales, however, cause the upper walls of the mines to be torn to ribbons, particularly in wet weather when the tissues get soaked and softened. Rain enters through the emergence holes of the adult beetles, and also by soaking through the walls.

### 7. Effect of Rain upon the Larvae in the Mines.

In periods of continuous wet weather, particularly if the leaves are lashed by strong winds at the same time so that they get wet on both sides, the rain enters the mines. The egg-capsules become saturated with water, which is then drawn into the narrow ends of the mines by capillary action through the slits by which the larvae entered the leaves on leaving the eggs. 1st-instar mines completely fill with water in this way. Larger mines do not fill completely by capillary action through the slits because their walls, towards the growing ends, are too widely separated; but water gradually soaks through the walls themselves, probably penetrating first through the stomata * in the dead tissue of the lower walls, and spreads over their inner surfaces until it accumulates at the ends, and then it gradually spreads from the ends until finally it wholly replaces the air in the mines and causes them to be distended. In these circumstances the contained larvae are entirely immersed in water and are prevented from breathing. So long as the rain continues the mines remain full, and if it continues long enough, as it occasionally does, the larvae are drowned. Evaporation of the water when the rain stops is comparatively slow, even in hot sunshine, because the water is nowhere directly exposed to the air; but even the largest mines become quite dry in about 12 hours, and small ones dry much sooner.

The larvae, however, can survive, to a remarkable extent, complete immersion in water for long periods. Extensive laboratory experiments showed that 1st-instar mines, when continuously immersed just beneath the surface of water, completely fill in 6 hours, and that the contained larvae, although rendered temporarily insensible, can survive immersion for 18 hours but not for 30 hours. Other experiments showed that if only the upper surface of the mines is kept constantly wet no water enters, even after 4 days. It is therefore the wetting of the lower surface which causes the entry of water, and it is only in heavy rain driven by strong wind that the lower surface becomes wet in the field. Large larvae, and pupae, are affected much more readily and more slowly by rain than 1st-instar larvae because their large mines fill much more slowly. (The significance of the drowning factor from the economic point of view is discussed later.)

Since temporary suspension of feeding results when the mines fill with water but do not remain full long enough for the larvae to be drowned, the tissues at the end of the mine die at such times through prolonged saturation, and subsequently dry before the larvae resume feeding. On these occasions, therefore, a line of callus tissue, visible externally, forms across the mine, and this is in every way comparable, except that it is usually rather less clearly defined, to the lines which mark the ends of the 1st and 2nd instar sections of the mine. These additional lines, which are due solely to the entry of water, give the impression that there are very frequently more than 3 larval instars; and some observers have actually stated, quite wrongly, that there are normally 4 larval instars, their observations having been based on counts of the number of lines across the mines after periods of exceptionally

* The stomata are confined to the lower surface.

wet weather. It is usually obvious, from the way in which the lines are spaced, which of them represent moults and which represent occasions when water has entered.

8. **Prepupa.** (Plates I and III.)

The prepupal stage is not a separate instar. It must be regarded as beginning when the full-grown larva ceases to feed and withdraws from the end of the mine, and it is terminated by the act of pupation. The prepupa is characterised by considerable distention of the thoracic segments and by a change in colour to a much paler yellow. These characters are first noticeable a day after the larva has withdrawn from the end of the mine. The distention of the thoracic segments results in a marked change in appearance of the individual as a whole, the increased dorso-ventral thickening, particularly in the 1st segment, causing lateral narrowing and consequent change of outline.

Throughout the prepupal stage the individual remains, unless disturbed, in that part of the mine to which it withdrew when it ceased to feed—namely, the 2nd-instar section or the beginning of the 3rd-instar section. Further excretion takes place during this period, but otherwise the individual is wholly inactive. The cessation of feeding causes the tissues round the edge of the wider end of the mine to harden, so that the mine now becomes sharply outlined all round its periphery on both surfaces of the leaflet, as at the moulting periods, while its walls at the wider end become increasingly brown as their tissues dry until finally the mine is uniformly brown throughout. In dry weather, the mine becomes wholly brown before the contained individual pupates, but in wet weather it usually remains green at the end until after pupation. The appearance of the mine, therefore, is not a reliable indication at this time of the stage of the contained individual.

9. **Pupa.**

Pupation takes place in, or just in front of, the 2nd-instar portion of the mine. The larval skin is completely shed and is readily visible in the mine. The pupa is not attached in any way. When first formed, it is yellow and soft-skinned, but within 6 hours its skin hardens and it acquires its permanent colour.

The orientation of the pupa is the same as that of the larva, its ventral surface being in contact with the upper epidermis of the leaf and its anterior end being directed towards the wider end of the mine. It is not subjected to pressure in the mine because of the bulging of the upper wall. The abdomen is curved longitudinally so that its ventral surface is on the inside of the curve. In this position, the dorsal surface of the abdomen is in contact anteriorly only with the mine wall, and the ventral surface is in contact only at its extremity.

The pnpa is capable of rapid movement, both backwards and forwards, along the mine, the movement being effected by rapid and regular contractions and extensions, alternately, of the abdomen. The spines on the dorsal surface of the abdomen and those at its extremity grip the walls and facilitate the progress of the pupa along the mine. In hot

sun the pupa occasionally moves along the mine, or wriggles without change of position; and a disturbance on the outside of the mine, or the penetration of the wall by the ovipositor of a parasite, causes it to move rapidly to another part of the mine. If a leaf containing a large number of pupal mines is tapped sharply, all the pupae move, and a plainly audible, rustling, sound results. Except in these circumstances, however, the pupa rarely moves, and it is nearly always in or near the 2nd-instar section of the mine.

About 5 days prior to the emergence of the adult beetle, the eyes of the pupa become dark brown, and 2 days later the mandibles also become dark brown. The wing-sheaths darken considerably 1½ days before the adult emerges.

10. **Adult.**

a. *Emergence from the Pupa.* When the adult is mature within the pupa, the sheaths of the appendages become detached from the body. A few hours later dehiscence occurs and the adult emerges from the pupal skin. The cast skin is very thin and transparent, but it retains its original form and its original position in the mine. The newly-emerged adult takes up a position a short distance in front of the pupal skin and remains motionless in the mine for 2 or 3 days (see pp. 51–52). It is orientated relatively to the mine in the same way as the larva and pupa. Its colour is at first pale straw throughout, except for the eyes and mandibles, which are black, and the elytra, which are dark distally, but while it rests within the mine its cuticle hardens and assumes its permanent colouring. About 12 hours after emergence the colouring is complete, but a considerable further period is required for the completion of the hardening process.

Emergence from the pupa occnrs at any time of the day or night.

b. *Emergence from the Mine.* In order to effect its exit from the mine, the beetle makes a broadly oval incision with its mandibles, almost invariably in the thin and brittle upper wall of the mine, cutting out a disc which usually drops to the ground but sometimes remains attached at one point or along one side so that it moves as though it were hinged (Plate IX, a). The long axis of the emergence hole is parallel to the veins of the leaflet, and the length of the hole is approximately 4·5 mm. The hole is nearly always situated at the end of the 2nd-instar section of the mine or the beginning of the 3rd. On account of its comparatively large size it is very conspicuous on the leaflet.

Very rarely, the emergence hole is in the lower wall of the mine. The beetle always makes the hole in that wall which it faces when it emerges from the pupa.

Emergence from the mine, unlike emergence from the pupa, almost always takes place at one particular time of day; namely, between sunrise and 9.0 a.m.

c. *Change in Colour and Texture of the Integument after Emergence from the Mine.* In addition to the colour change which occurs within the mine, there is also a further colour change which takes place very gradually after the beetle has emerged from the mine and while it is pursuing its normal activities. This further change consists in a darken-

ing of the integument and is particularly noticeable on the ventral surface. When the beetle first emerges from the mine, the ventral surface is light golden-brown in colour medially, from end to end, and this colour shades into very dark brown along the sides. After the beetle has been feeding for a few days, however, the whole of its ventral surface is either very dark brown or black. This final change is not completed until it has been feeding for either 3 or 4 days. In the course of field observations this colour change is often useful as a means of ascertaining whether the beetles have recently emerged or are already more than 3 days old.

d. *A Diurnal Insect.* The beetles are markedly diurnal, all their activities taking place by day only, in ordinary circumstances. At night they remain motionless on the leaves. They have been reported to spend the night on the ground, but such reports are quite erroneous. Their activities begin at sunrise and cease at dusk. The period of greatest activity is between sunrise and 11.0 a.m. Very occasionally the beetles are attracted to light at night, but only if the light is very bright and in their immediate vicinity.

e. *Locomotion.* The beetles are capable of flying as well as crawling, and flying is their principal means of locomotion. Nevertheless, they cannot be described as strong fliers. Their flight is slow and rather clumsy. They are capable of hovering in the air to some extent, and on hot sunny days they have a habit of flying slowly around the tops of the trees in large numbers. They are frequently seen flying from one tree to another nearby, and still more frequently from leaf to leaf of the same tree, but they appear to be unable to remain in the air for long and are therefore incapable of extensive flights. Apparently they cannot travel more than 100 yards or so at a stretch, except when carried by a strong wind. They have difficulty in taking wing from a flat, horizontal surface, and when about to fly, they make their way to some position, such as the end or edge of a coconut leaflet, or of a blade of grass if they are on the ground, which permits the wings to move without hindrance. After taking off from the ground, they rise almost perpendicularly into the trees above them.

The beetles spend most of their time on the undersides of the leaves and are essentially lethargic and slow in all their activities. They crawl slowly and deliberately over the leaflets when searching for a suitable spot in which to feed or lay their eggs. The broad, flattened, tarsal joints of the legs enable them to grip the undersides of the leaflets very tightly, and also to crawl with ease, upside down, on very smooth surfaces such as glass.

f. *Behaviour when Disturbed.* The beetles immediately drop from the leaves when touched, or disturbed in any other way. Also, any object which approaches close to them without touching them causes them to drop unless it approaches very slowly. If a leaf on which many beetles are feeding gregariously is tapped at the base they all drop off in a shower, but they take wing before reaching the ground even if the tree is a very short one. This habit of dropping is very characteristic, but it only occurs when the disturbance is of an unusual nature. The knocking together of the leaves and leaflets in a strong wind does not cause the

beetles to drop off. The habit clearly serves as a protection against predatory enemies, presumably lizards. The beetles are very conspicuous on the leaves on account of their brilliant colouring, particularly when they are feeding together gregariously, and they must be visible to lizards from considerable distances. If only one beetle in a large group is touched, all of them drop, so that all except one escape. It is interesting to note that the allied *P. nuciferae*, of Java, which is uniformly brown in colour, very inconspicuous on the leaves, and not gregarious, does not drop when disturbed. This suggests that the habit of dropping has arisen as a result of gregariousness in conjunction with conspicuous colouring.

g. *Influence of Light*. The beetles are extremely sensitive to light by day, and slightly by night, being attracted to those places where the light is brightest.*

Their response to light stimuli has far-reaching effects in the field, and is largely responsible for determining, in the initial stages of an outbreak, which trees are attacked. The phenomenon is most apparent in the case of a small area or "pocket" of coconut palms, some short and some tall, entirely surrounded and sheltered by forest. In such a place the tallest trees are in the full sun and are as brightly illuminated as trees growing in more open areas, but the smaller trees and those near the forest are in partial or complete shade. The beetles never feed upon the small trees, or the trees near the forest, in areas of this nature, except when the tall trees are already so heavily defoliated that there is little green tissue upon them. In all areas, however open and exposed they may be, the tall trees are always more heavily attacked, and trees near belts of forest are never attacked to the same extent except when the outbreak is so severe that the beetles are threatened with food shortage.

In big areas of coconuts, in which the palms are well spaced-out and there are no forest trees left standing, each palm is brightly illuminated on all sides. Such areas are always more severely and uniformly attacked than those in which the palms are growing close together or are interspersed with forest trees. It follows that those conditions which are most suitable for coconuts from all other points of view are also most suitable for the beetles. While many pests do more damage to trees which are planted too closely together, *Promecotheca reichei* favours those which are widely spaced, as they should be from other standpoints.

In the last stages of severe outbreaks, this response to light is not at once apparent, the movements of the beetles being influenced equally by other factors, but in the main it is very striking. It is readily demonstrated when a large number of beetles are released from the ground in an area of coconuts in which one or two trees stand separately but the majority are close together and form a more or less continuous roof. The crowns of the one or two more isolated trees are, as seen from the ground, surrounded by bright sky, and the beetles, when released, fly straight up to these trees and to no others, and the great majority fly directly to the same tree, which is often by no means the nearest but is always the most brightly illuminated.

h. *Influence of Wind and Rain*. A strong wind has little effect upon

* *i.e.* they are positively phototropic and heliotropic.

the beetles. It seems to cause them to hold on to the leaves more tightly than usual and to suspend their normal activities to some extent, but it does not dislodge them or induce them to drop off. Despite the tremendous lashing of the leaves which occurs in a strong wind, the beetles normally remain on the leaflets all the time, and they rarely attempt to fly. Those that do fly are quite helpless, on account of their weak and clumsy mode of flight, and they must often be carried considerable distances by the wind; but flight occurs so rarely in these circumstances that wind plays no significant part in the spread of the beetles, and there is never any appreciably greater spread in the direction of the prevailing wind than in any other.

The effect of rain on the habits of the beetles is equally slight. Light, and ordinarily heavy, rain has no effect upon them and they continue their normal activities all the time, even flying from leaf to leaf and tree to tree during the rain. Exceptionally heavy rain, however, causes the beetles to drop in large numbers to the ground in an exceptionally lethargic condition, particularly if it is accompanied by a strong gale which causes the leaves to become thoroughly wet on their under as well as their upper surfaces. The beetles cannot grip firmly on a constantly wet surface, and the incessant lashing of the leaves by the wind displaces them in these circumstances although it has no effect upon them ordinarily. It seems probable, also, that torrential rain continuing for a long time causes partial stoppage of the spiracles and consequent lethargy, although normal rain certainly does not penetrate to the spiracles. When the storm passes, the beetles gradually fly up to the trees again, and at these times swarms of them are sometimes seen together, flying slowly near the ground. This phenomenon is of rare occurrence, however, and it is the only occasion when the beetles are present in numbers on or near the ground.

i. *Feeding.* The feeding habits of the beetles are entirely different from those of the larvae.

About an hour after emerging from their mines the beetles are ready to begin feeding. They never feed upon the leaflets in which their mines are situated, and rarely upon the leaves which bear those mines. Instead, they fly about for a short time, and then settle upon a younger leaf of the same tree or upon a young leaf of another tree nearby. The tree chosen is not entirely a matter of chance. The beetles respond particularly readily when they are newly-emerged to light intensity and nearly always make their way to the tallest and most exposed trees at first.

The beetles normally feed only on the youngest leaves, and they show a marked preference for the distal thirds of the distal leaflets on those leaves. This applies to the males throughout their life. The females, however, while conforming to this rule for the first fortnight or so of their life, do not continuously conform to it subsequently. The desire to oviposit causes them to forsake the tips of the leaflets and to visit the older leaves as well as the youngest, and the short trees as well as the tall ones, so that after they have commenced ovipositing they no longer confine themselves only to the tips of the most exposed leaflets for feeding purposes.

Except at night, the beetles spend most of their time feeding, but they

stop frequently for short intervals and never resume feeding at the points at which they have ceased. Each one therefore makes several entirely separate feeding marks every day.

Feeding takes place only on the undersides of the leaflets. The exact method of feeding is peculiar and highly characteristic, and the resulting feeding-scars are readily distinguishable from those of all other insects attacking coconut palms in Fiji. The beetles do not mine in the leaflets nor eat right through them. They eat the lower epidermis and the green parenchymatous tissue, but do not penetrate the upper epidermis. When about to feed, a beetle wanders over the distal part of the leaflet, and having found a suitable spot it takes up a position such that its body is parallel to the mid-rib of the leaflet and its head is directed towards the base of the leaflet. It then turns its head to one side and tilts it backwards at the same time, so that the mandibles are no longer side-by-side, but one above the other. The mandible near to the leaflet is then thrust, in an antero-ventral direction relative to the beetle itself, into the tissues of the leaflet between two of the veinlets of the larger of the two series which lie near the lower epidermis. With the head still in the same position, the beetle then brings the other mandible down between the same two veinlets, thus biting out a very short length of tissue and making a minute longitudinal furrow in the leaflet. Having made this initial furrow, it advances to the end of it and thrusts its right mandible under the veinlet on the left or its left under the one on the right, and then, by bringing the mandibles together again like scissors, it cuts through the selected veinlet and in doing so doubles the width of the furrow. (This operation is only possible after the initial short furrow between the two veinlets has been made.) By constant repetition of the process of biting through the veinlet the beetle makes a long incision in the leaflet. It turns its head to the right and left alternately and regularly, the mandibles being thrust alternately beneath the veinlet, and after each bite it advances very slightly towards the base of the leaflet, but always pursuing the course of the same veinlet. Consequently, the incision is quite straight. At each bite, all the tissue as far as, but not including, the colourless layer of the upper epidermis is removed. The food of the beetles therefore consists of green parenchyma and the tissues of the lower epidermis and veinlets, but the parenchyma is the principal and the essential component, and the other tissues, which are removed only in order that the parenchyma may be reached, are subsequently discharged in the excrement, almost intact and only slightly digested. The width of the incision is greater inside the leaflet than at the surface, but at a given level its width is approximately constant throughout its length. The incision rarely includes a primary, secondary, or tertiary vein, and never includes any of the veinlets close to the upper epidermis. The main cross-veins are not devoured, and these are therefore visible in the incision as thick cross-strands at more or less regular intervals (Plates II, e and VII, b), but otherwise the depth of the incision is constant, being simply the thickness of the leaflet minus the colourless upper layer.

Since the veins and veinlets are all parallel and uniformly arranged, all the feeding-scars of the beetles on each leaflet are parallel and of

similar form and width, varying only in length (Plate VII, b). The surface width of a fresh incision varies from 0·17 to 0·20 mm. The length varies enormously, according to the duration of continuous feeding. In a typical, severely attacked, leaflet, selected at random, the length of the incisions was found to vary from 2 to 100 mm. The two ends of an incision always differ in that one is roughly square and the other is bluntly pointed (Plate II, e). The pointed end is the end at which the beetle began feeding, and it is therefore normally directed towards the tip of the leaflet, and the square end is the end at which it ceased feeding. The point is never on the middle line of the incision but is always an extension of one side, since it is formed by the initial bite of the beetle and therefore lies wholly on one side of the veinlet which is eaten away when the rest of the incision is made (Plate II, e). When an attacked leaflet is held up to the light, the feeding marks of the beetles are seen as thin white lines, each divided into sections of approximately equal length by the cross-veins, which appear black.

After a few days the tissues along each side of an incision become dry and die, and when two incisions are made close together, with only one veinlet between them, all the tissue between them dies. In a severe outbreak, when many beetles feed together on a single leaflet, the whole of the lower surface of the leaflet, except the proximal third, is covered with these incisions, all parallel and only separated by single veinlets. In such cases, the whole leaflet, except the proximal third, dies and becomes first brown, then grey, and finally, after much weathering, almost white, and the tip of the leaflet shrivels and curls over towards the lower side of the leaf (Plates XVIII and XIX).

It is interesting to note that the leaves of seedling palms are never attacked by *P. reichei*, which differs in this respect from *P. nuciferae* in Java. When forced in captivity to feed upon seedling palms, the beetles die in 3 days, although when provided, in otherwise identical conditions, with leaflets from tall trees they live very much longer. The leaf tissues of seedling palms, therefore, are not only unattractive to them but are actually fatal.

j. *Resting*. The beetles rest on the undersides of the leaflets. The resting attitude is characteristic. The body lies parallel to the mid-rib of the leaflet, and the head is usually directed towards the tip of the leaflet. The feet are splayed out on either side of the body, which is in contact ventrally with the leaf. The antennae are directed forwards parallel to the surface of the leaflet, and lie side by side, in contact with one another, throughout their basal halves; but distally they curve outwards, away from one another, so that together they have the appearance of a relatively long, two-pronged fork projecting in front of the head.

k. *Gregariousness*. The beetles are gregarious. As many as twenty may sometimes be seen feeding together near the extremity of one leaflet, although there are none on any of the other leaflets of that leaf. In view of the fact that there are about 200 leaflets on each leaf, this is remarkable. They are markedly gregarious, however, only during the period which precedes copulation.

We have already noted that *P. reichei* is normally an extremely local insect, and for this its gregarious habit is mainly responsible. The beetles

remain together in the trees in which they have emerged from the mines, and during the pre-copulation period they feed side-by-side on the same leaflets. Frequently they indulge in brief flights, but only around the trees in which they have been feeding, and after these flights they again collect in groups in the same trees.* After pairing has occurred, however, and throughout the oviposition period, the gregarious tendency, though still in evidence to a slight extent, is very much less marked, and the beetles no longer collect in large groups, although for the most part they remain in the same trees. The restriction of the species, generation after generation, to one tree or to a few trees is very characteristic, and even in severe outbreaks, when the beetles are compelled to spread to new areas, their reluctance to do so until they must is always very noticeable.

l. *Pairing.* Pairing does not take place until the females are nearly a fortnight old, and until they attain this age, they are completely ignored by the males. When the beetles are common, every individual of both sexes pairs many times during its life, and pairing, having commenced, occurs once nearly every day in the remainder of the life of every female, and occasionally twice in one day, until the female ceases to oviposit. Frequent pairing is, however, wholly unnecessary for the fertilisation of the eggs, as females which have paired only once oviposit normally and all their eggs are fertile, and the sex-ratio of their progeny is normal. The duration of the act of copulation varies from ½ hr. to 3 hrs. Females which have had no opportunity of pairing commence to oviposit at the usual time, but their eggs invariably fail to hatch, parthenogenesis being unknown. In normal conditions, however, pairing always takes place, and no infertile eggs have ever been found in the field.

m. *Oviposition.* Every female commences to oviposit within 4 days after it has paired. The precise duration of the total pre-oviposition period (from emergence from the mine) is discussed on p. 53, and it is sufficient here to note that it covers abont 2 weeks, but varies considerably. The females begin ovipositing in the trees in which they have been feeding, and since the tallest trees are preferred for feeding purposes in the pre-oviposition period, the number of eggs laid in those trees is greater than in any others. If only a few beetles are present, they lay all their eggs in the tall tree or trees in which they have been feeding, but in severe outbreaks, the beetles are so numerous that they kill the tips of all the leaflets of the taller trees before they begin to oviposit and are then forced to descend, in increasing numbers day by day, to the smaller trees for food, and in these circumstances they oviposit almost as extensively in the smaller trees as in the tall ones.

As in all their other activities, the beetles, when ovipositing, confine themselves to the undersides of the leaflets. In selecting leaflets for oviposition purposes they do not conform to the rules which apply to the selection of leaflets for feeding purposes. In fact, the leaflets on which eggs are chiefly laid are the very ones which, in general, are not used for food. While the leaflets preferred for food are those in the distal third or half of each leaf, those preferred for egg-laying are in the proximal half

* In the special conditions prevailing in severe outbreaks, sudden and periodic spreading to new areas occurs, but this cannot be regarded as a normal habit of the species. It is discussed separately in Section IV, B.

of the leaf, and although, in severe outbreaks, some eggs are laid on all leaflets, the great majority of eggs, and therefore mines, are always concentrated in the proximal half of the leaf. Moreover, the tips of the leaflets are largely avoided for oviposition purposes, and this applies as much to those which are healthy as to those which the beetles have damaged by feeding on them. Still another very marked preference which the beetles show when ovipositing is for that half of each leaflet which is on the proximal side of the mid-rib.

When the beetles are plentiful, the eggs are very uniformly distributed over the leaflets, within the limits defined above. The number of eggs per leaflet is approximately constant, and the eggs are, for the most part, widely separated from one another.* This is due to the avoidance by the beetles when ovipositing of the close proximity of other eggs. Each beetle, before laying an egg, makes a general survey of that part of the leaflet on which it finds itself and, on finding an egg, moves away from it. This habit is always very noticeable, except in abnormally severe outbreaks, and clearly serves to lessen the chances of the resulting mines meeting. However severe an outbreak may be, the number of eggs laid on each leaflet of the youngest, previously unattacked, leaves is very rarely in excess of the number of larvae which each of those leaflets can nourish. The number of eggs on each leaflet of the older leaves in severe outbreaks always greatly exceeds the number of larvae which each leaflet can nourish, but this is due to the fact that the older leaves have been attacked by more than one generation of beetles so that many of the eggs on them belong to earlier generations and have long since been dead, having died as a result of the attacks of parasites and predators. The proximity of old, dead, eggs is not avoided by the beetles when ovipositing, and consequently the number of eggs increases as the age of the leaves increases, and it is necessary to distinguish between the eggs of different generations in judging the habits of the beetles when ovipositing in bulk.

Another respect in which the beetle exhibits a tendency to select those sites which are most favourable for its progeny is in the avoidance of dead tissue, such as other mines, and even the proximity of dead tissue. It is at once able to distinguish between living and dead areas, and even when mines are very abundant, so that only 25% of the area of each leaflet remains green, eggs are very rarely laid on them. In severe outbreaks, many eggs are to be seen on the dead tissue of old mines; these, however, have not been laid on mines, but have been undermined subsequently by larvae from other eggs laid earlier.

The female lays its eggs singly, and there is only one egg in each capsule. The habits of the beetle when ovipositing are peculiar and interesting. It wanders up and down the selected leaflet for a long time before deciding exactly where to lay its egg. Having chosen a suitable site, it applies its mouth-parts several times to the surface of the leaflet, appearing to bite the epidermis, although actually the latter is not ruptured or damaged in any way whatsoever. Careful removal of a large number of recently-laid eggs failed to reveal any trace of fracture in the epidermis, and there seems no doubt that the beetle merely cleans the surface, probably removing epidermal hairs, in order to ensure close

* The number per leaflet is discussed on p. 100.

adherence of its egg. Certainly no secretion is deposited on the leaflet during this operation. In any case, whatever its purpose may be, this preliminary operation is invariably performed, and having performed it, the beetle proceeds to take up a position such that its head points towards the proximal end of the leaflet and the tip of its abdomen lies over the spot to which the mouth-parts were applied. It feels the leaflet with the tip of its abdomen, the latter being moved rapidly and irregularly over the surface, until it finds the exact spot, and it then lays its egg exactly on that spot. The feeling process appears to serve to ensure that the end of the abdomen is in the right position, as the presence of epidermal hairs on the surface of the leaflet would at once be detected by contact with the numerous hairs associated with the external genitalia. The preliminary cleaning operation and the egg-laying together occupy about 2 minutes.

The formation of the covering capsule begins immediately the egg is laid. Without changing its position the beetle waves its abdomen rapidly and regularly from side to side over the egg and as it does so it deposits on the top of the egg a viscous mass which contains many fragments of semi-digested leaf tissue. The fragments are principally epidermal, and mostly parallel-sided. This deposit is apparently identical with the normal excrement of the beetle. The waving motion of the abdomen serves to distribute the viscous mass uniformly over the surface of the egg; it consists, not only in a rapid movement from side to side, but also in a much slower backward-and-forward, swaying motion of the whole body, which begins as soon as the excrement is deposited. The deposition of the excrement takes place in one act, but it is followed continuously, though very slowly, for about 10 minutes, by the expulsion of a less viscous, light-brown, liquid, in which no solid particles are suspended. Throughout this time the two independent movements of the body are continued and when eventually the exudation ceases the egg is completely and uniformly covered. At this stage the beetle invariably turns round so as to face the egg and proceeds to pat it all over with its fore-legs in a very ludicrous manner. It then gradually moves over the egg, repeating the patting first with the middle-legs and then with the hind-legs. It then turns right round and repeats the whole process again and again. The patting undoubtedly serves to press the capsule, which is still viscous, more closely against the contained egg. Having done this the beetle walks off and soon flies to another leaf. The viscous fluid very soon dries to form a tough kind of cement which binds the excretory fragments very firmly together and is a very effective protection against most predatory and parasitic insects.

Oviposition continues for about 2 weeks, and during this period the beetle lays at least one egg every day, and frequently, particularly on hot, sunny days, it lays 2 eggs in one day. Very rarely, 3 eggs are laid in one day, and the maximum is 3, but this only occurs when no eggs have been laid on the previous day. In continuous hot, sunny weather, eggs are laid every day; 2 is the maximum for one day in these circumstances, and the maximum rate of oviposition (*i.e.* 2 per day for 2 or more successive days) is usually reached 8 days after the commencement of oviposition (*i.e.* just after the middle of the oviposition period) and is usually main-

tained for 3 days but sometimes for only two. The average number of eggs laid per day during the oviposition period is approximately 1·5. The egg capacity (*i.e.* the number of eggs actually laid, not the number in the ovaries) varies from 16 to 25, and the mean is approximately 20, so that the average number of mature eggs produced by each ovariole is 2 only, though actually some ovarioles undoubtedly produce 3, while others produce only one. This estimate of the egg capacity and of the rate of oviposition was obtained, not only by daily observations of beetles in large cages (6 ft. high × 3 ft. × 3 ft.) but also by a very large number of dissections of females of estimated age collected in the field and by actual observation of the beetles, in bulk and singly, in the field. The use of cages in different positions, and of leaves from trees of different ages for food, showed that the beetles oviposit to the maximum extent only when they can obtain abundant sunlight, frequent but intermittent moisture in the form of dew or rain, and leaves of normal thickness and maturity for food. Estimates of the period of oviposition in the field are comparatively simple, because, in most severe outbreaks, the majority of beetles emerge within a few days of one another and it is easy to see approximately when oviposition begins and ends in bulk in each generation and in any given area. Field observations of the number of eggs laid by each female per day are not difficult, but are very tedious. For obvious reasons, only those beetles which descend to small trees can be constantly watched, and only those small trees which are so situated that the beetle population in them is very small (preferably one only), and is not constantly changing, can be used for this purpose. The method of dissection of females of estimated age (based on a knowledge of the date when bulk emergence began), and collected in the field, serves only to indicate, with a wide range of error, the maximum number of eggs which are available for laying in one day and the rate at which eggs are produced, because the eggs develop gradually and successively, not simultaneously, and therefore this method is useful only in conjunction with others. Rough estimates of the maximum possible egg capacity are simple, because field observations alone in one-stage outbreaks are sufficient to show that the duration of the oviposition period does not exceed 3 weeks and that individuals lay less than 2 eggs per day on the average. This means that the egg capacity certainly does not exceed 35 and is probably less than 30. Accurate estimates of the actual egg capacity, however, can be obtained only by a complicated combination of the methods outlined above, and this shows not only that the true figure is less than 30 but also that the mean is actually about 20 only.

The very low egg capacity (20), and the short duration of the oviposition period (2 weeks), are remarkable when this species is compared with the Java species, *P. nuciferae*, the habits of which, while differing in several important details, are, in general, the same.

n. *Post-oviposition Period.* There is always a short post-oviposition period before the beetle dies. During this period, the duration of which varies from 2 to 4 days, the beetle continues to feed normally except for about the last 24 hours of its life, when it ceases to feed, becomes lethargic and drops to the ground.

o. *Spreading.* The apparently sudden occurrence of severe outbreaks

of this pest, in localities that have formerly been free from outbreaks for a long time, has led to the belief in Fiji that the beetles migrate in considerable numbers and over long distances. The question of the origin of outbreaks is discussed in Section IV, and it is sufficient here to remark that the idea that they originate as a result of migration has proved to be wholly erroneous.

Actually, the beetles are incapable of extensive migration. They are indigenous and usually well controlled on islands which have a fringe of coconuts all round their coasts; and on any such island they have only to move a little further down the coast to find fresh food, for however seriously they may have defoliated the trees in one locality, neighbouring localities are always free from them or less defoliated. Even if all the trees on a particular island were seriously defoliated, the defoliation, for reasons explained in Section IV, could never be so complete that the beetles were absolutely without food and were compelled to migrate to another island for that reason, or to die in the attempt. It is therefore certain that the beetles are not only physically unable to fly long distances, but are also under no necessity to do so in natural circumstances. Moreover, no matter how dense their population may be, they never make any concerted attempt to reach new areas or show any tendency to collect in swarms to do so. Except in the case of small islands separated from one another by only a few hundred yards, no spreading from island to island ever occurs.

In certain circumstances, however, which only arise in the course of severe outbreaks, the beetles spread in enormous numbers from the trees or the area in which they emerged from their mines to neighbouring trees or adjacent areas which have not previously been attacked. This is not mass migration, but is rather in the nature of a haphazard spreading which continues for a long period and in which each beetle behaves entirely independently. Although many thousands of beetles often take part, no stream of beetles is to be seen invading the new area, and the only evidence of the invasion is the gradually increasing abnndance of the beetles in the trees which were not previously attacked. The beetles spread by short flights from tree to tree, and from day to day, not by single long flights. The special circumstances in which these migrations take place are important. We have already seen that the beetles are strongly gregarious in the pre-copulation period, and that during the rest of their lives, when the gregarions tendency is greatly diminished, they are nevertheless very reluctant to spread. The result is that no appreciable spreading occurs from an infested tree or area for several generations. There comes a time, however, when the condition of maximum possible defoliation and of maximum population (see Section IV) within that tree or area is reached, and it is at this time, and not before, that migration commences. Until they have paired, the beetles present at this time remain within the original area, and are markedly gregarious as usual, but having paired, they begin to fly to neighbouring, unattacked, trees and no longer show any strong tendency, even after they have reached new trees, to remain where they are. There is no definite direction of migration, and, unless there are natural barriers, the beetles spread in all directions equally. Each stopping-place, of each individual,

itself becomes a starting-point from which the individual again spreads, and from which it may spread in any direction, including that from which it has come. Thus, back-migration into the original area takes place to some extent, and the beetles concerned in it set out a second time on their wanderings, while others proceed at each flight further away from the original area. The spreading ceases only when all the beetles have laid all their eggs and have died. In one-stage outbreaks spreading necessarily takes place periodically only, at long intervals of several months; and since the period during which adult beetles are present is approximately the same in every generation, the furthest distance through which the beetles spread is always approximately the same on all occasions when spreading occurs and is equal to the distance traversed by those beetles which spread continuously away from the original area. This distance is usually about 200 yards on estates in which the trees are spaced in the usual way and in which there are no barriers in the form of hills, belts of forest, or in any other form; but it is liable to vary greatly when the spacing of the trees varies or when there are natural barriers.

The beetles are capable of crossing narrow belts of forest or short stretches of sea when they are spreading to new coconut areas, but they do so in very small numbers, relatively, so that the resulting outbreaks in the new areas develop much more slowly than they would if those areas were continuously connected with the original ones by coconut palms. Belts of forest which are only 20 yards wide are effective barriers to a remarkable extent, but never completely. Hills, unless they are entirely covered with coconuts, and clearings which are more than about 50 yards wide, also serve as partial barriers. There is, therefore, a very noticeable tendency for *P. reichei* to be confined within natural boundaries, and to a much greater extent than in the case of more active pests.

It is necessary to note that the term "migration" is misleading if applied to this insect. It suggests, though it does not literally mean, a concerted flight of the beetles *en masse* to distant localities, the intervening areas not being attacked by them. Actually, no mass flights ever take place, and the spreading which does occur is characterised, as we have seen, by a marked lack of gregarious tendencies. Moreover, the beetles never spread across an area of coconut palms without attacking them, but move only from one area to another directly adjacent to it except when they cross natural barriers which contain no food for them.

The spreading of the species by agencies other than the powers of locomotion of the insects themselves is discussed later.

p. *Duration of Adult Life.* The beetles, of both sexes, live for approximately one month. In captivity, the maximum duration of adult life in large cages was 30 days. A rough estimate is readily obtainable by field observations of the beetles in bulk in one-stage outbreaks, for it is easy to see when they first appear in bulk in a given area and when they disappear in bulk, but it is important to ascertain with certainty that their disappearance is due to death and not to spreading. In the case of females, the adult life may be regarded as consisting of two distinct periods—a pre-oviposition period, which is devoted to gregarious feeding and later

to pairing also, and a period which follows the commencement of oviposition and is devoted to oviposition and more solitary feeding. The duration of each of these periods proves to be approximately 2 weeks.*

The duration of adult life, being approximately one month for both sexes, is comparatively short for a coleopterous insect, and is very short as compared with that of the allied *P. nuciferae* in Java.

q. *Sex Ratio.* The sex ratio was determined by collecting about 2,000 mined leaflets at random in the field at Nabavatu in August, 1933, when the pupal stage was the dominant one in the severe one-stage outbreak which was then raging. The leaflets were all placed in large cages, and the beetles were removed every day, as they emerged, and the sexes counted. Eventually, almost all the mines produced beetles, and the sex-ratio, as thus determined, was undoubtedly representative of the species. The number of males which emerged was 1,107, and of females 974. From these figures, the sex-ratio is :—

$$♂ : ♀ = 1{\cdot}14 : 1{\cdot}00.$$

Thus, the sexes occur in nearly equal numbers, but males slightly predominate.

Collecting the adult beetles with nets in one-stage outbreaks is less satisfactory as a means of ascertaining the sex-ratio, unless the collecting is carried out during the pre-copulation period. At all times after copulation has occurred, the females tend to spread to new areas more than the males, so that an abnormal predominance of males occurs in the old areas and of females in the new. Early in June, 1933, 744 beetles were collected with a net in a very severely attacked area at Nabavatu after oviposition had commenced; of these, 437 were males and 307 females, and this gives the sex ratio as $♂ : ♀ = 1{\cdot}4 : 1{\cdot}0$, which is accurate for that particular time and place, but is not accurate for the species as a whole because many females had already spread to new areas.

### G. Life Cycle, Duration of Generations, and Rate of Multiplication.

Two methods were adopted for determining the rate of development and the duration of each stage. First, observations of marked individuals in the field were made twice daily, from the time when the eggs were laid to the emergence of the adult beetles from the mines. This method consists solely in observations made from outside the mines, the mines remaining unopened and in their natural positions on the trees. Secondly, the exact times at which the various moults occurred were determined by direct observations in the laboratory of the larvae and pupae inside the mines, which were opened and closed again for the purpose; the leaflets containing the mines were kept in water, and the larvae, whenever necessary, were inserted into fresh leaves artificially. These methods are described in detail in Section IX.

In addition, determinations of the duration of the adult life, and of

* Exact figures are given on p. 53.

the various periods into which the adult life is divided, according to the activities of the beetles, were made by observations of beetles in cages and by observations of the beetles *en masse* in the field in one-stage outbreaks.

The two seasons in Fiji are very different climatically, particularly as regards temperature and rainfall. Since the rate of development of insects varies greatly with temperature, it was necessary to make all these observations twice, in the coolest months of the cool season and the hottest months of the hot season. The cool, drier, season, during which the south-east trade wind prevails, extends roughly from May to October inclusive; and the hot, wetter, season from November to April inclusive. The transition from season to season, however, is gradual and no sharp limits can be defined.

The rate of development in the cool season was determined at Nabavatu during July, August, and September, 1929. The rate in the hot season was determined in the same locality during January, February, and March, 1934. In each case, 200 individuals were used, and observations of each *individual separately were made twice every day.* The records thus obtained are condensed in Tables II and III below :—

*Table II. Life Cycle of* P. reichei.

(The figures are days.)

| Period. | Cool Season. | | Hot Season. | |
|---|---|---|---|---|
| | Range. | Mean Duration. | Range. | Mean Duration. |
| Incubation | 17–20 | 19·0 * | 14–16 | 15·0 |
| 1st-Instar Feeding | 8–11 | 9·2 | 6–10 | 8·1 |
| 1st Resting (including 1st moult) | 5–9 | 7·5 | 5–7 | 6·3 |
| 2nd-Instar Feeding | 7–12 | 9·0 | 6–10 | 7·8 |
| 2nd Resting (*including* 2nd moult) | 5–9 | 6·8 | 5–7 | 6·0 |
| 3rd-Instar Feeding | 11–16 | 12·9 | 10–13 | 11·0 |
| Prepupal | 5–8 | 6·2 | 3–5 | 4·2 |
| Pupal | 15–19 | 17·7 | 11–13 | 12·1 |
| Adult Resting (spent in Mine) | 3–5 | 3·9 | 2–4 | 3·4 |
| Total (Oviposition to Emergence from Mine) | 86–93 | 92·2 | 71–78 | 73·9 |

* The incubation period in the cool season was again checked in July, 1933, 25 eggs being used. The variation on this occasion was found to be 17–22 days, and the mean was 19·3 days.

The larva resumes feeding approximately 24 hours after each of the two moults. Each of the two long resting periods may therefore be divided into a pre-moulting and a post-moulting period of about 6 days and 1 day respectively in the cool season and about 5 days and 1 day respectively in the hot season. The life cycle may be more simply expressed in the following manner :—

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*Table III. Life Cycle of* P. reichei.

(The figures are days.)

| Period. | Cool Season (Mean Duration). | Hot Season (Mean Duration). |
|---|---|---|
| Incubation . . . . . . | 19·0 | 15·0 |
| Larval (including Prepupal) . . | 51·6 | 43·4 |
| Pupal, with Period spent in Mine by Adult . . . . . . . | 21·6 | 15·5 |
| Total (Oviposition to Emergence from Mine) . . . . . . | 92·2 | 73·9 |

It is important to note that the total range (86–93 and 71–78 days) recorded at the bottom of Table II is obtained, not by adding the figures above it, but by direct observations on individuals reared right through from egg to adult, regardless of the intermediate stages.

The average figures for the total duration (*i.e.* 92·2 and 73·9 days, is obtained by adding the figures above it and was confirmed by observations on individuals reared from egg to adult, regardless of intermediate stages.

A study of these two tables reveals the following facts, which we shall have occasion to refer to later :—

i. The total duration of the life cycle (*i.e.* 92·2 and 73·9 days) is remarkably long for a tropical insect which becomes so numerous as to be regarded as a pest.

ii. The range in the total duration (*i.e.* 86–93 and 71–78 days) is very small for such a long period, especially in view of the fact that the individual stages vary considerably.

iii. For general purposes the total duration of the life cycle from oviposition to emergence of the adult may be regarded as covering 3 months in the cool season and $2\frac{1}{2}$ in the hot.

iv. There is great seasonal variation in the rate of development. This is due solely to temperature changes. The difference in mean temperature between the hottest and coolest months of the year at Nabavatu is approximately 10° F., and this causes a difference in the period of the life cycle (oviposition to emergence from the mine) of no less than 18·3 days (92·2 minus 73·9). This means that the period of the life cycle is increased by about 25% by a fall in mean temperature of 10° F., and by nearly 2 days by a fall of 1° F., within the normal temperature limits which prevail in Fiji.

The duration of the 1st- and 2nd-instar feeding-periods is liable to be very greatly increased by unsuitable food, and the total duration of the larval period and of the whole life cycle in such cases is correspondingly lengthened. Drought is the most usual cause of unsuitable food, but unsuitable soil conditions have the same effect as far as the larvae of *P. reichei* are concerned. Whatever the cause may be, the leaf tissues, particularly the veins, become abnormally hard, and the young larvae are unable to bite through the primary, secondary, or tertiary veins and therefore cannot widen their mines in the usual way. In consequence, the larvae have insufficient room for their normal movements when

feeding and cannot obtain an adequate food supply, and their mines become greatly attenuated. The 1st instar suffers most in this respect, on account of its small size and comparative weakness, and the 3rd instar is not affected at all, and develops at the normal rate, being large enough and strong enough to overcome the hardness of the veins. The 400 individuals whose rates of development are summarised in Tables II and III all fed on normally healthy trees, and the range in the 1st- and 2nd-instar feeding-periods shown in the tables is the normal range, and does not include larvae which have fed in unsuitable leaves. Separate records were, however, obtained for these abnormal cases, and these show that the 1st-instar feeding-period may be lengthened to no less than 21 days, and the 2nd-instar feeding-period to 15 days, without detriment, ultimately, to the individuals concerned. It is only in severe outbreaks that eggs are laid on trees which are suffering from adverse conditions sufficiently to cause abnormally slow development of the larvae which result from them, and only a few trees here and there are affected adversely to this extent. Even in times of exceptional drought, at least 90% of the larvae develop at the rate shown in Tables II and III, and those which develop abnormally slowly are nearly all in young trees, which are affected far more than old ones.

It is now necessary to consider the duration of the life of the adult female, after emergence from the mine, and the durations of the various periods into which the adult life may be divided. These latter periods are four in number, and are enumerated in Table IV below, their durations having been determined in the cool season of 1933 and the hot season of 1933–34 :—

*Table IV. Adult Life of* ♀ P. reichei.

(The figures are days.*)

| Period. | Cool Season. | | Hot Season. | |
|---|---|---|---|---|
| | Range. | Mean Duration. | Range. | Mean Duration. |
| Pre-copulation Period . . | 12–15 | 13·0 | 10–12 | 10·5 |
| Copulation to Oviposition . . | 2–4 | 3·0 | 2–4 | 2·5 |
| Oviposition Period . . . | 11–16 | 14·0 | 11–14 | 12·0 |
| Post-oviposition Period . . | 2–4 | 3·0 | nil | 2·0 |
| Total Duration of Adult Life (*after Emergence from* Mine) . . . . | 27–35 | 30·0 | 25–30 | 27·0 |

* The figures for the range are correct to the nearest day, and those for the mean to the nearest half-day.

These figures are based mainly upon observations of beetles in cages. The total duration of the adult life of males was found to be exactly the same as that of females, both in the field and in cages. The pre-copulation period of males was not accurately determined, but it was ascertained that they do not become sexually mature earlier than the females.

From Tables III and IV it is clear that the mean for the period which elapses between the laying of an egg and the time when the individual

resulting from that egg commences to oviposit is 108 days in the coolest months and 87 days in the hottest months, and that the mean total duration of life, from the laying of an egg to the death of the resulting individual, is 122 days in the coolest months and 101 days in the hottest. The *duration of one generation must be regarded as the period which elapses* between the laying of an egg and the middle (not the beginning) of the oviposition period of the resulting individual, and this is 115 days in the cool season and 93 days in the hot. Since the seasons are of approximately equal duration, the mean for the year is 104 days (3·5 months) and the number of complete generations per annum is 3·5. When the insect occurs in non-outbreak condition, or in multiple-stage outbreaks, it is obviously impossible to observe the number of generations per annum directly, because all stages are present simultaneously, the generations overlapping completely. In one-stage outbreaks, however, the generations can be observed directly, since an almost complete lack of overlapping is maintained indefinitely; and in these outbreaks the number of generations per annum, as directly observed, is always very nearly or exactly 3·5. A single example will suffice. At Tota, on the island of Vanua Balavu, prepupae were the dominant stage on April 26th, 1933. They were dominant next in August, then again early in December, and again on March 10th, 1934. On April 26th, 1934, one year after the first observation was made, eggs were the dominant stage. Thus, in one year there were 3 complete generations and part of a fourth, the part being 47 days (March 10th–April 26th), which is almost exactly half a generation in the hotter months. The prepupal stage is particularly suitable for observations of this nature because it is comparatively short and its period of dominance, being correspondingly short, can be represented with sufficient accuracy by a single date.

Since the egg capacity is 20, the mean duration of one generation 3·5 months, and the sex ratio 0·47 (♂ : ♀ = 1·14 : 1·00), the rate of multiplication per generation, in the absence of controlling factors, is 9·4, and the population after any given time is obtained by the formula: $p' = p \times 9{\cdot}4^n$, where $p'$ is the required population, $p$ is the initial population, and $n$ is the number of generations in the given time $\left(n = \frac{\text{time in months}}{3{\cdot}5}\right)$. The following table shows the population resulting from a single average female for the first 6 generations, in the absence of controlling factors :—

*Table V. Potential Rate of Multiplication of* P. reichei.

| Generation. | Months. | Males. | Females. | Total. |
|---|---|---|---|---|
| I | 3·5 | 10·6 | 9·4 | 20 |
| II | 7·0 | 100 | 88 | 188 |
| III | 10·5 | 933 | 827 | 1,760 |
| IV | 14·0 | 8,766 | 7,774 | 16,540 |
| V | 17·5 | 82,404 | 73,076 | 155,480 |
| VI | 21·0 | 774,606 | 686,914 | 1,461,520 |

Thus, a single female can give rise to one and a half million, approximately, in 6 generations, or 21 months.

## III. PARASITES AND PREDATORS ASSOCIATED WITH *P. REICHEI* IN FIJI (PRIOR TO 1933).

Several species of parasitic insects, primary and secondary, are associated with *P. reichei* in Fiji, and there are also a few predators that attack it, and a few insects and mites that visit the mines but do not attack their occupants. A complete list of all these is given below :—

*Oligosita utilis*, Kow.
*Elasmus hispidarum*, Ferr.
*Tetrastichus taylori*, Ferr.
*Eupelmus* sp.
Eupelmid (near *Anastatus*).
*Pediculoides ventricosus*, Newp.
Ants.
Lizards.
Coccinellids.
Mites (other than *P. ventricosus*).
An Attid Spider (*Ascyltus pterygodes*, Koch).
" Parasite A."
A Fungus.

*O. utilis* and *E. hispidarum* are indigenous Hymenopterous parasites. *T. taylori* and the two Eupelmids are hyperparasites, all Hymenopterous and presumably indigenous. *P. ventricosus* is a parasitic mite, of almost world-wide distribution and certainly not indigenous in Fiji. Another species of mite occasionally feeds as a predator on *P. reichei* and on the Hymenopterous parasites, and there are at least two other mite species which live in the mines but are only scavengers. Ants, lizards, and the Attid spider, attack *P. reichei* as predators. Coccinellids do not attack *P. reichei*, but frequently utilise its mines for sheltering their eggs. " Parasite A " is extremely rare as an enemy of *P. reichei* and is known only from its cocoon. The fungus is entomogenous.

This is probably a complete list, and as such it is comparatively short. Its shortness is due mainly to the limited fauna of Fiji, and to the very specialised habits of *P. reichei*. The presence of only two primary Hymenopterous parasites, other than the rare "Parasite A," is noteworthy. Birds have never been observed to attack any stage of *P. reichei*. It is most probable that the adult beetles are occasionally attacked by birds, but if this does occur, it is certainly an extremely rare event, and of no importance.

### A. *Oligosita utilis*, Kow.*
(Trichogrammatidae.)

**1. Hosts.**

*Promecotheca reichei*, *P. bicolor*, and *P. opacicollis*.

It is most probable that this parasite has no hosts other than *Promecotheca* spp.

* *Chaetostricha cratitia*, Watrst.

## 2. Distribution.

Fiji (including Futuna), and New Hebrides. *O. utilis* appears to be present on all the larger islands in Fiji. In the Lau Group it is present not only on all islands but also in all localities, and it is abundant in every outbreak of *Promecotheca*; in other parts of Fiji, it is not invariably present at any one time in all localities where its hosts occur, and its incidence is very erratic.

Since it attacks *P. bicolor* as well as *P. reichei*, it is present in the

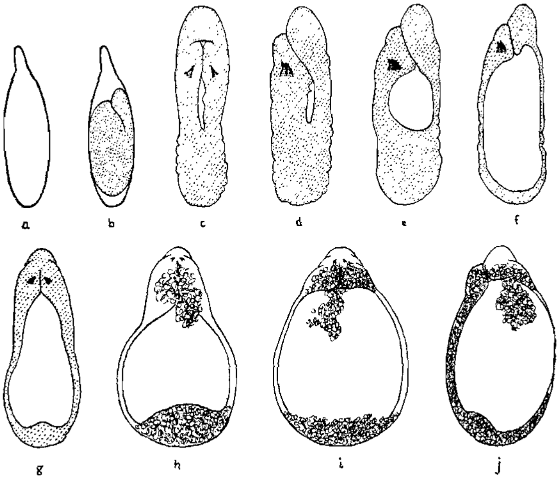



FIG. 8.—*Oligosita utilis*: egg, and early larval development. a, outline of egg (× about 120); b, egg with contained larva contracted prior to hatching (× about 120); c, newly-hatched larva, dorso-ventral view (× about 144); d, ditto, left lateral view; e, larva, left lateral view, 1 hour after hatching (× about 144); f, larva, left lateral view, 2 hours after hatching (× about 128); g, ditto, dorso-ventral view; h, larva, 3 hours after hatching, dorso-ventral view (× about 104); i, larva, 4 hours after hatching, dorso-ventral view (× about 80); j, ditto, left lateral view.
(All as seen by transmitted light, without compression; slightly diagrammatic.)

forests on many islands as well as in the coconut areas, but in the Lau Group, where *P. bicolor* is absent, it is confined to the coconut areas.

## 3. Description of Stages.

a. *Egg* (fig. 8). The egg is extremely minute and delicate. It is absolutely transparent and colourless, and can only be detected with the

greatest difficulty when the host eggs are dissected. It varies slightly in shape, but its shape is always approximately as in the figure. The narrow extension is at the anterior end. The mean length is 0·27 mm.

b. *Larva* (fig. 8 and Plate X). The newly-hatched larva is elongate and roughly cylindrical, its diameter being almost the same throughout its length. The posterior end is bluntly rounded. The anterior end, when the larva is viewed dorso-ventrally, appears similar to the posterior end; but when the larva is viewed laterally, it is seen to be constricted, ventrally only, at the mouth, which is not at the anterior extremity, so that the anterior end is a relatively large lobe which projects in front of the mouth. Segmentation is entirely lacking, both internally and externally. The skin, particularly in the posterior half, is wrinkled transversely, and this sometimes gives an impression of segmentation. There are no cuticular processes, or appendages of any kind. The mandibles are black and very sharply pointed; they are visible as a pair of minute dots just behind the mouth. The gut is an elongate sac, almost empty and consequently very slender, terminating at about the middle of the larva. The length of the newly-hatched larva is 0·26 mm.

The larva changes completely in appearance as soon as it begins to feed, but the change is not effected by moulting. There are no moults at all until pupation, and the whole of the larval period is therefore one instar. Growth is rendered possible solely by the capacity for distention of the much-wrinkled skin of the newly-hatched larva. A parallel case is the inflation of a balloon, and the newly-hatched larva is not unlike a deflated balloon in appearance, while the fully-grown larva definitely resembles a fully-inflated one. The mandibles and the cephalic lobe are the only structures which are incapable of distention or growth, and in the full-grown larva they appear ridiculously small in consequence.

The commencement of feeding results immediately in the distention of the gut, which becomes pear-shaped owing to greater distention in its posterior half. At the same time the posterior half of the larva as a whole begins to swell, and the wrinkles in the skin disappear. The gut then continues to expand until its walls are in contact at the sides with the body-wall, and the larva itself is then pear-shaped, being slightly constricted just in front of the middle. The constriction, however, is soon lost, because the anterior part of the gut, and consequently of the larva itself, now expands, so that the larva assumes a broadly ovoid form; and very soon the gut completely fills the body except for a small space anteriorly and another posteriorly. Almost the whole of the surface of the gut is now in contact with the body-wall, and this condition is maintained throughout the extensive growth which follows.

The larva, at this stage, is an ovoid, tightly distended, sac, with the cephalic lobe projecting as a small papilla anteriorly. The skin is absolutely transparent and exceedingly shiny and smooth. The colour of the larva is bright, translucent, yellow, being due to the contents of the gut, and the larva as a whole resembles a drop of oil or a bubble. This appearance is maintained until the larva is full grown, except that as growth proceeds the papilla appears to shift further and further on to the ventral surface, owing to more rapid expansion anteriorly and dorsally than elsewhere, and the contents of the gut gradually change from a

homogeneous yellow fluid to a mass of yellow globules which appear first in one or two patches only, but later almost wholly fill the gut. Throughout this later growth, the posterior half of the larva remains almost hemispherical and the anterior half is slightly narrower, but equally rounded. The dorsal surface is more convex than the ventral. The mouth is situated on the papilla, close to its posterior edge; and just behind the papilla, the minute mandibles, which are necessarily still the same size as in the newly-hatched larva, are always visible as black dots.

In the next stage, following the completion of feeding and growth, numerous white spots appear, and are distributed all over the body. Actually, the spots are situated in the wall of the gut. At first there are only a few, but they rapidly increase in number. They are opaque, white, bodies, of non-cellular structure. Their origin and function is not clear, but they are probably associated with the elimination of waste products. They are always very conspicuous, and are very characteristic of the stage which intervenes between the cessation of feeding and pupation.

At the time of appearance of the spots, the larva is still tightly distended. Soon afterwards, however, a great change in appearance takes place. The body contents shrink considerably, and this results in great wrinkling of the skin. The wrinkles are mainly longitudinal and are much more numerous dorsally and laterally than ventrally. At the same time, the larva, while maintaining its former length, becomes much narrower and, at the anterior end, more pointed. It also becomes more opaque. The region of the mouth is smooth and shiny, and behind this smooth area, which is situated antero-ventrally, there are 3 transverse furrows, which, however, do not represent the beginning of segmentation. There is no segmentation, internally or externally, and there is no tracheal system. Towards the end of this stage, the white spots, although still as large and as numerous as before, become much less apparent because the fat-body increases greatly in extent and bulk.

The size of the full-grown larva varies greatly, but the maximum length is about 1·10 mm. The size depends upon the number of individuals per host. The shape, except when the larva is in the fully distended stage, also varies very greatly, since the cuticle is entirely without rigidity, and the larva is capable only to a very small extent of controlling its own shape.

The stage just described is terminated by the development of the rectum and the act of excretion, and the following stage may be regarded as prepupal.

c. *Prepupa.* The prepupal stage is very similar to the stage which immediately precedes it. The dorsal and lateral surfaces, however, are even more wrinkled, while the ventral surface is now entirely without wrinkles and very smooth, except for a few transverse furrows towards the posterior end, which appear to represent the commencement of segmentation. The posterior end is now narrower and more pointed than the anterior end. The white spots are now lacking; they completely disappear at the time of excretion. The parasite is still bright yellow except at the two extremities, which are transparent and colourless. The abdomen exhibits definite internal signs of segmentation in addition to the external furrows. The original mandibles and papilla are still

present, and the anus is visible posteriorly and ventrally. There is still no tracheal system.

d. *Pupa* (Plates V and XI). The pupa is bright yellow and translucent, and its surface is very shiny and absolutely smooth. The cuticle is excessively thin, fragile, and perfectly transparent. The shape varies considerably, owing to pressure from other pupae in the same host. Usually, the dorsal surface is nearly flat and the ventral surface convex, the convexity being due to the fact that the ventral surface is usually in contact with the wall of the host egg. The sutures are not clearly defined, and the segmentation of the abdomen is scarcely apparent. The length of the pupa varies, according to the number per host, from 0·68 mm. to 1·08 mm.

e. *Adult* (Plate XI). The adult was originally described by Kowalski (*Ann. d. Epiphyties*, **4**: 302, 1917), and again later, under the name *Chaetostricha cratitia*, by Waterston (*Bull. Ent. Res.*, **13**: 184, 1932).

The sexes are similar, but are readily distinguishable even when alive, by the following characters :—

i. Males are always smaller than females from the same host individual.

ii. The external genitalia, which are readily visible.

iii. The last two abdominal tergites of the male are brown, so that the end of the abdomen appears dark in colour; the female is yellow throughout.

## 4. Life History.

*Oligosita utilis* is an egg parasite. It attacks eggs of any age, but shows a marked preference for those recently laid. Its progeny can mature if the host eggs are attacked within the first two-thirds of their incubation period, but if the host eggs are older than this the parasites usually die as larvae, their food supply being insufficient and unsuitable on account of the advanced stage of development of the host embryo. The number of eggs laid in each egg of *P. reichei* almost always exceeds 2, bnt varies from 1 to 10, and is most frequently either 3 or 4. The maximum number of parasites which can mature in one egg of *P. reichei* is 6, and the minimum is 1. The eggs of *O. utilis* are not attached to the chorion of the host egg, but lie entirely free in the yolk.

The young parasite larva, when mature within its egg, contracts longitudinally, and this causes pressure on the chorion. A longitudinal split occurs in the chorion and the larva is immediately discharged. The actual discharge is purely mechanical, and is not due to any activity of the larva itself. The larva, even at this stage, is extraordinarily inert, being quite incapable of any movement except extremely slow and almost imperceptible contractions and expansions. The mandibles play no part in hatching; it appears that the only purpose they serve is puncturing the embryonic tissues in the host egg, and even this is very often unnecessary because the majority of the parasites find themselves in recently laid eggs, whose contents are almost wholly fluid. At the time of hatching, the mandibles are non-chitinised, delicate, and colourless, but very soon after hatching they become strongly chitinised and hard, and from this time onwards they remain unchanged.

Feeding commences immediately the larva escapes from the egg. The food is absorbed with great rapidity, so that the initial form of the larva is lost almost at once. At the time of hatching the gut is a minute, nearly empty, sac in the centre of the body, but 2 hours after hatching it has expanded so that it comes in contact with the body-wall, and the larva has begun to acquire the pear-shaped form already noted; and 4 hours after hatching, the gut almost completely fills the body and the larva is tightly distended and of globular form. Until this time the gut contains a homogeneous, transparent, fluid, but the yellow globules, to which reference has already been made, now begin to make their appearance and the gut becomes less transparent. The larva now measures 0·51 mm. in length, and therefore nearly doubles its length and completely changes its form in 4 hours.

The rate of development of the parasites is somewhat slower than this in host eggs in which the embryos are already in a fairly advanced stage of development, presumably because the food is less readily assimilated and the parasites are obliged to rupture the tissues with their mandibles.

Until the larva is full grown, no further change takes place, except in size and in the extent of the yellow globules in the gut. The maximum size is reached, and the contents of the host egg are completely devoured, about 3 days after the eggs hatch, but the exact period varies. Hitherto, the larva has been surrounded by fluid, but from this time onwards it is surrounded by air. No tracheal system develops, however, respiration being solely apneustic in both media. The larvae in each host egg (Plate V, a) are packed closely together, and they are enclosed by the vitelline membrane, the chorion, and the capsule, of the host egg. The drying of the vitelline membrane and chorion, resulting from the absorption of the normal fluid contents by the parasites, causes parasitised eggs from this stage onwards to have a very different appearance and to be readily distinguished from healthy ones. On account of the covering capsules, the host eggs themselves are not visible *in situ* on the leaf, but they can very easily be displaced and turned over by means of a needle inserted under the edges of the capsules and levered gently away from the leaf surface. The under surface of a healthy egg is then seen to be uniformly deep-yellow in colour and tightly stretched, while that of a parasitised egg is whitish and dry in appearance, and usually somewhat wrinkled. This means of distinction is of great value in the field. When the chorion and vitelline membrane of a parasitised egg, turned over in this manner, are dissected away, the parasite larvae are fully exposed and can be removed from the egg, but they always adhere to some extent to the membrane; and this adhesion, together with the extreme fragility of the larval integument, renders the operation somewhat delicate if the larvae are to be removed without fracture.

The larva, when full grown, as when newly-hatched, is very inert; and it is absolutely incapable of any movement or change of shape, except that the mandibles occasionally undergo slow forcipate movements, and the mouth region, in the centre of which is the cephalic papilla bearing the mouth itself, is partially withdrawn into the body from time to time so that the papilla comes to lie in the centre of a small depression.

The white spots, already described, begin to appear very soon after the larvae have completely devoured the host contents and become full grown. They are always present in larvae 4 days old. Very soon after they first appear, the shrinkage of the body contents commences and the wrinkles begin to form in the skin. Prior to this stage, development is exceedingly rapid, as has been shown; but the subsequent development is very slow, and the changes which lead up to excretion and the prepupal condition cover at least 3 weeks from the first appearance of the spots, while the previous development covers only 4 days from the hatching of the egg. Pupation occurs a few days after excretion, but the precise period was not satisfactorily determined. The time that elapses between the cessation of feeding and pupation varies very greatly (from 3 to 5 weeks), even in the same conditions of temperature and humidity, but the usual period is approximately a month. Since the act of pupation is the first moult, the whole of the long period which precedes it is one instar, and this is divisible into a feeding period of 3 days and a non-feeding period of 27 days (mean).

The shrinkage of the body contents, and the consequent wrinkling of the skin, proceed continuously, though very slowly, throughout the long non-feeding period until excretion takes place. In consequence, the larva, which is tightly distended at the beginning of this period and therefore incapable of change of shape, becomes increasingly pliable towards the end of the period so that its shape is influenced to a considerable extent by contact with the wall of the host and with the other larvae present. Further, it becomes capable, to a very small extent, of changing its shape independently, the body frequently undergoing local and very slow contractions and expansions, without regularity or symmetry. To this extent only is it capable of movement, and at no time is it able to move, as a whole, to a new position.

The excrement is deposited as an insignificant, irregular, yellowish mass at the posterior extremity of each individual, and when pupation takes place the old larval skin is thrust back and crumpled up against the excrement, where, on account of its extreme thinness, it soon becomes quite invisible.

The pupae are usually orientated so that their ventral surfaces face the egg capsule, rather than the leaf, and are in contact with the wall of the egg. Therefore, when the adults emerge they find themselves facing the capsule, through which they must bore, with the aid of their mandibles, in order to escape. They always rest, however, for about 3 days, during which the integument hardens, before attempting to escape. They eventually escape by biting neat, circular, holes in the capsule (Plate V, b). Often all the parasites use the same exit hole so that there is only one hole in the capsule, but 2 or 3 holes are frequently made. The number of holes, however, rarely equals the number of parasites previously present in the egg. The exit holes are conspicuous and very characteristic, serving as a ready means of detecting the presence of this parasite in any locality. They cannot be confused with the more irregular holes made by ants, and there is nothing else with which they could be confused. (When *P. bicolor* is the host, the parasites always escape by biting through the epidermis of the leaf, not through the capsule. This is due to the different

structure of the capsule of *P. bicolor* (p. 223) and to the fact that *P. bicolor* sinks its eggs into the leaf tissues.)

Almost invariably, the parasites in each host egg include one male, but there are seldom two or more. Consequently, the sexes occur in very unequal numbers and females always predominate in the field. The *majority of eggs yield either 3 or 4 parasites, and the sex ratio is therefore* approximately 2·5 : 1 in favour of females. Actually, the sex ratio was found at Nabavatu to be : ♀ : ♂ = 2·8 : 1 (380 ♀♀ and 134 ♂♂ from about 150 eggs collected in the field from several trees). This ratio is undoubtedly typical, and it means that the number of parasites per egg is more often 4 than 3.

Pairing usually takes place on the day of emergence from the egg, but it may take place at any subsequent time. Parthenogenesis rarely, if ever, occurs in nature. The adult life is long. In captivity, nearly all females lived for 3 weeks, the majority lived for more than a month, and one lived 7½ weeks. The males live at least 2 weeks, but never so long as the females. The adults are often to be seen wandering over the leaves with a rapid, erratic movement, which is characteristic. There is a short pre-oviposition period varying from 3 to 5 days, but otherwise oviposition proceeds slowly, almost daily, throughout life, if a constant supply of host eggs is available. When about to oviposit, the female first crawls all over the egg-capsule for some time, making a preliminary survey, and then thrusts its ovipositor through the capsule and into the contained egg. The female at once recognises and avoids those eggs which have already been attacked, so that superparasitism rarely occurs.

### 5. Life Cycle.

The incubation period was determined accurately in the hot season, and was found to be 33 hours at a mean temperature of 85° F. for the 2 days concerned (max. 89° F., min. 81° F.). In the cooler season it is longer, bnt it is always less than two days.

The larval instar varies very greatly in duration, but the mean period in the hot season was found to be 30 days.

The pupal period is approximately 3 weeks.

The duration of the total life cycle, from oviposition to emergence from the pupa, varies greatly, mainly on account of the variation in the larval period. The minimum was found to be 42 days (in the hot season) and the maximum 62 days (in the cool season), and the mean in the cool season was found to be 58 days at a main daily temperature for the whole period of 78° F. (max. 87° F., min. 70° F.).

The life cycle is therefore very long for a tropical parasite of this type. Its length, together with the length of the adult life, enables the parasite, in one-stage outbreaks of *Promecotheca*, to survive in large numbers the long period (about 9 weeks) when no eggs of the pest are present.

### 6. Natural Enemies.

*Oligosita utilis* is liable to be attacked by *Pediculoides ventricosus* and by ants. The former is rare as a natural enemy of this parasite as it can only enter the egg through fractures in its under surface (*i.e.* the surface in contact with the leaf), and fractures very seldom occur. Ants,

on the other hand, destroy *O. utilis* in enormous numbers, and materially lessen its usefulness in outbreaks of *Promecotheca*. There are no secondary parasites.

B. *Elasmus hispidarum*, Ferr.

(Elasmidae.)

1. **Hosts.**

*Promecotheca reichei* and *P. bicolor*.

It is noteworthy that *E. hispidarum* is exceptional among species of *Elasmus* in that its hosts are Coleopterous. The genus *Elasmus* as a whole has Lepidopterous hosts.

It is almost certain that this species has no hosts other than *P. reichei* and *P. bicolor*. It does not attack Lepidopterous or Dipterous leaf-miners.

2. **Distribution.**

*Elasmus hispidarum* is distributed throughout Fiji wherever its hosts occur. With one exception, no outbreak of *P. reichei*, however small, has ever been found without it in any part of the Group, and it is present alike in the wet and the dry zones. In normal climatic conditions, it may be assumed to exist in all coconut areas, except on small islets. In the forests it is present, in association with its other host, *P. bicolor*, on Viti Levu, Vanua Levu, and probably on all the Lomaiviti islands (Ovalau, Koro, etc.), but it is not present in the forests of the Lau Group on account of the absence of *P. bicolor*. In Taveuni, *P. bicolor* has never been found and is probably absent, and therefore *E. hispidarum* is probably confined to the coconut areas in Taveuni, as in Lau.

3. **Description of Stages.**

a. *Egg* (Plate XII). The egg is translucent, colourless, smooth and shiny. The long axis is slightly curved, and the ventral surface, when the egg is viewed laterally, is almost a straight line. Both ends are uniformly rounded, but the anterior end is broader. The length varies from 0·39 mm. to 0·43 mm., the mean length being 0·42 mm.

b. *Larva*. 1st Instar (Plate XII). In the newly-hatched larva the segmentation is very distinct. There are 13 segments in addition to the very large head. The greatest width is at the 3rd and 4th segments, behind which the body tapers almost to a point. When the larva is viewed laterally, the back is seen to be strongly convex, while the ventral surface is straight. The head is smooth and very shiny, but all the body segments appear rough, the roughness being due to innumerable raised points which are distributed thickly and uniformly all over the skin, and extending all over the dorsal and lateral surfaces but not on to the ventral surface; the back and sides, therefore, are not shiny, but the ventral surface, like the head, is very shiny. Mid-ventrally there is a row of 7 fleshy, intersegmental, retractile, protuberances, functioning as pseudopodia, the first being between the 2nd and 3rd segments and the last between the 8th and 9th. Unlike the full-grown larva, the 1st-instar larva has no dorsal pseudopodia. Each of the first 3 segments bears ventrally a pair of fleshy protuberances one on each side of the line of the

pseudopodia. There are invariably only 4 pairs of spiracles, situated on segments 2, 4, 5, and 6. The mouth-parts are situated on a lobe which protrudes from the head ventrally. Total length of 1st-instar larva, when extended and before commencement of feeding = 0·38 mm. Width of head varies from 0·09 mm. to 0·11 mm.

The full-grown 1st-instar larva appears very different from the newly-hatched larva because the great increase in size causes separation of the points which constitute the roughness, and consequently the skin becomes shiny. The raised points are, however, still readily visible under the microscope, and they, as well as the width of the head, always serve for the recognition of the 1st instar.

2nd Instar. The skin in the 2nd instar is absolutely smooth and shiny. There are still only 4 pairs of spiracles. The width of the head, just after the first moult, is variable, but is approximately 0·15 mm. This instar is readily distinguishable from the 1st by the smoothness of the skin, and from the 3rd by the presence of only 4 spiracles.

3rd Instar. This instar is very similar to the 2nd, but the full complement of spiracles (9 pairs) is now present. The width of the head, just after the 2nd moult, is approximately 0·23 mm.

4th (last) Instar (Plate XIII). The 4th-instar larva has 13 segments in addition to the head, and the segmentation is very distinct even when the larva is full grown and extended. The segments are all nearly equal in length. The anterior end of the body is broadly rounded, the posterior end pointed. The head is situated antero-ventrally. The 13th segment, which bears the anus, is very small and elongate and is retractile into the 12th. The skin is absolutely transparent, smooth, shiny, and colourless. The general colour of the larva is either yellow or brown, according to the state of preservation of the host, being due solely to the contents of the gut. There are 9 pairs of spiracles, on the 2nd to the 10th segments inclusive. Along the centre of the back is a row of pseudopodia, one in each intersegmental space. These project as short, transverse ridges. There is a similar row of pseudopodia mid-ventrally; these are larger but less numerous, being present in the 3rd to the 7th intersegmental spaces only. All the pseudopodia are retractile and are protruded only when the larva is fully extended. They serve to enable it to move about in the mine, and in this respect they are assisted by the extremity of the 13th segment, which serves as a sucker. The mouth-parts and associated structures are shown in fig. 9. There is a pair of antennae, a pair of ocelli, and a pair of sensory pits representing palpi. The antennae are simple papillae, unsegmented, but they are slightly chitinised and brown throughout. The positions of the microtrichia are constant, as shown. The shape of the mandibles, which are heavily chitinised, is very similar to that of many other external parasites, but the almost straight point, together with the outline of the basal structure, as figured, is characteristic. There is a pair of short cuticular thickenings supporting the mouth and presumably serving also for the attachment of muscles; the shape and dimensions of these are characteristic.

Each body segment bears one dorsal pair and two lateral pairs of microtrichia, the laterals of each side lying one above the other. The 1st segment bears, in addition, another pair of dorsal microtrichia, the 4

dorsals on this segment lying approximately in a transverse row. All the microtrichia are exceedingly minute.

The size of the fully-grown larva varies very greatly according to the number of individuals per host and the size of the host. The largest individuals, however, when fully extended, measure 3·40 mm. in length.

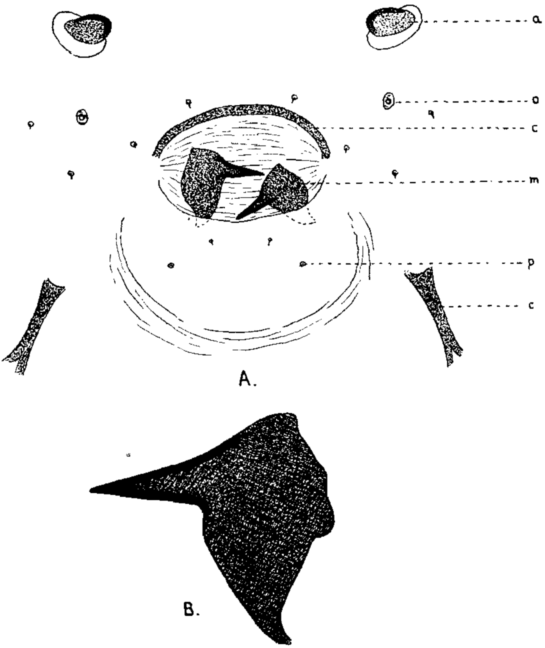



FIG. 9.—*Elasmus hispidarum.* A, mouth-parts and associated structures of full-grown larva; B, mandible. a, antenna; c, cuticular thickenings; m, mandible; o, ocellus; p, sensory pit.

c. *Prepupa* (Plate XIII). The prepupa, which is white, translucent, and shiny, is of very characteristic shape. The markedly tapering thoracic half is particularly noteworthy. The thoracic segments are very large and perfectly smooth. The anterior abdominal segments are much wider

than the thoracic but are very short, and all the abdominal segments are slightly wrinkled transversely.

d. *Pupa* (Plate XIII). The pupa is of elongate form and of a light, translucent, yellow-brown colour. (It becomes black and opaque shortly before the contained adult emerges.) The surface is very shiny and absolutely smooth. The abdomen is very long and tapers regularly almost to a point, and the hind leg-sheaths extend just beyond its extremity. Other noteworthy features are the sharply-pointed projections at A (Plate XIII) and the forked process at B. There are no markings. The pupa varies greatly in size, the largest pupae attaining a length of 3·2 mm., while the smallest are 1·7 mm. long.

e. *Adult* (Plate V). The adult is described by Ferrière in *Stylops*, **2**: 91, 1933 (Chalcidoid and Proctotrupoid Parasites of Pests of the Coconut Palm). The sexes are very readily distinguishable on account of the 3 very long branches of the male antennae.

4. **Life History.***

*E. hispidarum* is an external primary parasite of the larva. It attacks larvae of all ages equally readily, but never attacks pupae. The egg, larval, and pupal stages of the parasite are all passed within the mine, but outside the host.

The adult parasite oviposits in mines in which the larvae are feeding, not in those in which the larvae are resting for moulting. Oviposition is effected by the penetration of the wall of the mine, always on the underside of the leaf, by the ovipositor, but the act of oviposition is always preceded by a long preliminary investigation of the mine and by the stinging of the host. The parasite wanders incessantly over the mine, np and down, and from side to side, usually in the central part of the mine a long distance, relatively, from the contained larva which is feeding at the end. From time to time it inserts its ovipositor into various parts of the mine, but no eggs are laid and the ovipositor does not remain for long in the mine. This preliminary investigation often lasts for half-an-hour or more. Sooner or later, however, the parasite finds the larva at the end of the mine. It then takes up a position over the larva and inserts its ovipositor through the wall of the mine, pushing it very gently and gradually through the puncture until it comes into contact with the skin of the larva. It then makes a sudden stab, by bending its legs so as to bring its body close to the leaf, penetrating the skin and withdrawing the ovipositor instantaneously. This always causes the larva to cease feeding and to withdraw from the end of the mine. Sometimes the larva is only stung once, but on other occasions the parasite follows it down the mine, and, after locating it exactly by constant vibration of the antennae in contact with the mine, stings it again. The larva is usually stung at the side of the thorax, but not invariably, and the result of the stinging is to render it lethargic, so that it makes no attempt to move again. It is not normally killed. If it is removed from the mine and touched with a needle, it wriggles energetically, although normally it remains motionless within the mine. The principal effects of the stinging

* This section is based on observations with *P. reichei* as host, but there is no doubt that it applies in all essentials when the host is *P. bicolor*.

appear to be a general lessening of sensibility and complete paralysis of the head, including the mouth-parts. The larva does not die until after the young parasite larvae, which result from the eggs laid after the stinging operation, begin feeding upon it.

After stinging the host, the parasite immediately proceeds to oviposit. It does not choose any particular part of the mine for this purpose. The ovipositor is inserted at any point, and this time it is thrust in as far as possible; that is, until the abdomen is in contact with the leaf surface. The parasite remains in this position, with the ovipositor inside the leaf, for several minutes, often for 15 mins., and during this time the eggs are deposited in an irregular group inside the mine. They are often placed in contact with the paralysed host, but equally often they are a long distance from the latter, and they may be embedded in the dried excrement which lines the mine along each side. They are readily visible *en masse* as a white dot when the mine is opened, and a single egg is just visible to the naked eye. The eggs are not attached in any way, but their very shiny surface is always slightly moist, so that they adhere to one another and to objects with which they are in contact, although they can readily be removed with a needle or displaced by a sharp tap upon the mine.

The number of eggs laid in each mine depends upon the size of the host, the parasite invariably suiting the number of eggs laid to the food-supply available for the resulting larvae. 1st-instar larvae of *P. reichei* can just support 2 parasites, and occasionally 2 eggs are laid in 1st-instar mines, but usually there is only one. In 2nd-instar mines, the number of eggs varies from 2 to 6, and in 3rd-instar from 6 to 18; 18 being the maximum observed and probably representing the maximum possible at one time, since there are 6 ovarioles, and dissections showed that there are never more than 3 fully-developed eggs at one time in any one ovariole. It is possible for 18 parasites to mature on one large 3rd-instar host.

The eggs all hatch at approximately the same time, often all within half-an-hour and always within 2 hours. The empty egg-shells are extremely delicate and transparent, and are slightly crumpled in the process of hatching, but they can usually be detected because they are very shiny. The young larvae immediately proceed to wander in the mine in search of the host. Their movements are very slow and deliberate, although facilitated by the pseudopodia and the roughness of the skin. The larvae wander incessantly in all directions, and in large mines they often fail to find the host for many hours, and some never find it and die of starvation. If they are unable to find the host they die after wandering for 30 hours. Very frequently, however, the larvae, on hatching, find themselves on, or very near, the host, in which case they start feeding almost immediately. They cannot feed on the hard, chitinised, prothoracic segment, but the skin of all other parts is soft and the parasites can penetrate it readily. They begin feeding wherever they first reach soft skin. When the parasite begins feeding a sort of pumping action is evident in its head, this being due to its efforts to penetrate the skin. The pumping action ceases after a few minutes, and subsequently the head remains motionless and the only movement is the usual wave-like movement of the gut as the food is absorbed.

It is the feeding of the young larvae that ultimately causes the death

of the host. When feeding commences, the host twitches slightly occasionally, but it usually dies within 12 hours from the commencement of feeding by the parasites, and always within 24 hours.

The growth of the parasite larva is exceedingly rapid. Six hours after the commencement of feeding, its appearance is entirely different, owing to tight distention of the skin and the absorption of the yellow body-fluid of the host. The distention causes the larva to be much less supple, and it frequently projects straight out from the surface of the host, being attached only by its mouth. It moults 3 times in the course of its growth, so that there are 4 larval instars. Feeding is absolutely continuous in ordinary circumstances, except during the 3 moulting periods. Each of these 3 periods is very short and occupies about 2 hours only. The cast skins are usually invisible, being exceedingly flimsy. They adhere in a crumpled condition either to the parasite or to the host. After each moult, the parasite moves very slightly so as to resume feeding at a different point on the host skin, but except on these occasions it does not move until it is almost full grown, when it is often compelled to move for more food because it completely empties the host skin locally.

As the parasites feed, the body contents of the host become increasingly liquid, and eventually the host skin is completely emptied although it is not ruptured anywhere except for the minute punctures made by the mandibles of the parasites. Typically, the body-fluid of the host remains in a good state of preservation to the last, without even changing in colour, but frequently decay sets in and the host, and consequently the parasites, acquire a dark brown colour. This decay, except in extreme cases, merely causes slightly slower growth of the parasites and is not ultimately detrimental to them.

As soon as they have emptied the host skin, the parasites leave it and wander in the mine preparatory to pupating. The time that elapses between the hatching of the eggs and the cessation of feeding is normally about $3\frac{3}{4}$ days only. The larvae wander to all parts of the mine after they have emptied the host skin. After about an hour, they cease wandering and do not move again. About 28 hours after the cessation of feeding, they excrete, no excretion having taken place previously. The excrement is deposited in a single, lumpy, brown mass against the wall of the mine. The act of excretion marks the beginning of the prepupal period. Pupation takes place about 20 hours after excretion. The pupa is attached to the excrement, and therefore to the wall of the mine, by the larval skin, which persists in the form of a thin and twisted, white, thread, one end of which is attached to the excrement and the other to the posterior extremity of the pupa (cf. *D. javanica*, Plate XIV, c; the mode of attachment is identical in the two cases). The pupa is not attached at any point except by the larval skin, and is therefore merely suspended in the mine, but it is usually held in place by the close proximity of the walls of the mine and by the dried excrement of the host.

The emptied host skin persists as a dry, shrivelled mass. It is readily visible when the mine is opened because the hard prothoracic plates retain their normal shape and colour, and remain shiny.

The emergence of the adult parasite from the pupa takes place at any time during the day or night, but most frequently in the afternoon. It is

followed by a resting period, spent in the mine, during which the parasite remains motionless and its exoskeleton hardens. The duration of the resting period is usually about 24 hours, but varies from 18–36 hours. Adults which emerge from the pupae early in the morning usually emerge from the mines during the following morning, but those which emerge from the pupae in the evening sometimes do not leave the mines until the early morning of the next day but one. Emergence from the mines takes place at any time during the day, but never at night. All the parasites in one mine usually emerge from the pupae on the same day, and the males are usually, but not invariably, a few hours before the females.

Emergence from the mines is effected by biting a perfectly circular hole in the upper or lower wall of the mine; the former being much more usual, presumably because it is very much thinner. Usually, all the parasites in one mine emerge through one hole, but sometimes 2 holes are made. It is usually a male which makes the hole, but since the hole is only just large enough for it to emerge, and since the males are always smaller than the females of the same batch, the first female always has to enlarge the hole before it can escape. As soon as one female has escaped, the others follow, as a rule, in quick succession. The making of the hole occupies a period varying from 1–3 hours, and the parasite works at it almost continuously; and after the emergence of the male, the enlargement of the hole by the first female may occupy another hour.

Pairing normally occurs immediately the females emerge from the mine. It never occurs within the mine, although in 3rd-instar mines there is plenty of space. The male waits close to the hole in the mine for the females to appear, constantly waving its antennae over the hole. As soon as the head of a female appears, the male becomes greatly excited; and immediately the female escapes from the mine, and before it has time to crawl away, the male pounces on it and pairing takes place, occupying only a few seconds. The actual act of copulation is always preceded by a very brief courting performance on the part of the male, which takes up a position on the back of the female and strokes the antennae of the latter with its own, the stroking being accompanied by a rhythmic and rapid bowing movement of the male's body. As soon as pairing is completed, the male returns to the hole to await the next female. One male can pair with many females in quick succession, and almost invariably all the females are paired as soon as they emerge. When, as is sometimes the case, several males emerge from one mine, they all wait at the hole, disposing themselves radially around it with their heads almost in contact, and when a female appears a strenuous fight ensues amongst the males. Occasionally all the individuals in one mine are females, and in other cases there is only one parasite per mine. In these circumstances pairing may not occur until several days, or even weeks, after emergence. Both sexes can pair at any time during their long lives, but only one pairing is necessary to ensure the fertilisation of all the eggs. Parthenogenesis seldom occurs in normal circumstances, but it can occur, and always produces males only.

The adult life of females is long. In 1929, and again in 1933, records of more than 50 days were commonly obtained for females which were not given any opportunity to oviposit. The maximum record in 1929

was 56 days and in 1933, 62 days. Females which are constantly provided with mines in which to oviposit live approximately one month, but not longer. Males live approximately 3 weeks. All these records were obtained from females kept in glass tubes and fed regularly with honey, and there is good reason to believe that they represent the normal periods of adult life in the field. The nature of outbreaks of *P. reichei* (Section IV) is often such that *E. hispidarum* has to face a period of approximately 6 weeks. at the end of each generation of the pest, when no larvae are available for it to attack. A high percentage of the parasites fail to survive this long period, and die without issue, but many do survive, nevertheless, and attack the young pest larvae of the next generation very heavily. as soon as they appear, the attack continuing for about 10 days and then abruptly ceasing. This means that the last of the parasites from the previous generation of *P. reichei* larvae live for about 52 days.

The females are often to be seen in the field wandering over the leaves in search of mines, but the males are rarely seen. Both sexes fly extensively, but feebly. If suitable hosts are constantly available, oviposition is almost a daily occurrence throughout the life of the female. The effective egg-capacity for large females, as estimated by laboratory observations of the actual numbers of eggs laid each day by known females throughout their lives, is approximately 50. There is, however, a short pre-oviposition period varying from 2 to 3 days. (The rate of oviposition is very similar to that of *D. javanica*, Section VI, f, which was investigated with greater accuracy in this respect.)

The sex ratio varies according to the stage of the host individuals attacked, except when all stages are present simultaneously. When the predominant stage of the host is 1st-instar, in which case there is only one parasite per mine as a rule, males are more numerous than females in the proportion of 7 : 5. On the other hand, when 3rd-instar larvae predominate females are more numerous than males in the proportion of 2 : 1. The ratio for individual 3rd-instar mines varies enormously, but there is almost always at least one male per mine. When only 1st-instar mines are present, pairing cannot usually take place on emergence, there being only one parasite in most of the attacked mines; and the excess of males in these circumstances tends to compensate for the otherwise diminished chances of the sexes meeting.

The size of the adult parasites varies very greatly, according to the number of parasites per host and the size of the host.

The stinging of the host and the effect upon the host, as we have described them, are to be regarded as typical. In very many cases, however, the parasite fails to paralyse the host in the mine but nevertheless oviposits, and, in other cases, when the host is stung it dies, decays, and dries prematurely. These occurrences, although definitely abnormal, are very frequent in the field, as well as in the laboratory, and they account for an extensive wastage of eggs.

The failure to paralyse the host is usually due to the fact that the parasite is unable to locate the host in the mine, as can be observed readily if the mine, with the parasite upon it, is held up to the light or if the mine is observed *in situ* in the tree against a bright sky. The *Promecotheca* larva, not having been affected by the abortive attempts of the adult

parasite to sting it, is able to prevent the young larvae from commencing to feed by displacing them, and often crushing them, against the wall of the mine as soon as they attempt to do so. The host wriggles energetically, and even if some of the parasites have taken up positions between its segmental protuberances so that they cannot be displaced by contact with the mine, they are prevented from feeding, even though they sometimes succeed in penetrating the skin, by the incessant movement of the skin relative to the body-wall and the contained organs. It is, in fact, essential for the parasites that the host should be paralysed.

The premature death, decay, and drying of the host is particularly common when the host is in the 1st instar, although it occurs in all instars. Whether it is due to mechanical injury caused by the sting, to excessive injection of the toxic fluid, or to the entry of fungi or bacteria through the puncture, we do not know. However this may be, the host dies long before the eggs of the parasite hatch, and if it is small it often shrivels and dries almost completely soon after the parasite larvae have commenced to feed, and the latter die in consequence. In larger larvae, no extensive shrinkage or drying takes place before the parasite eggs hatch, but decay has already set in; and the parasite larvae, although capable of surviving considerable decay in their food, cannot survive the excessive pollution which occurs in these circumstances. The fact that 1st-instar larvae are far more susceptible in this respect than older larvae is attributable simply to their much thinner skins and small body contents, which cause them to be less resistant to all adverse external factors.

It is often assumed that a parasite which paralyses its victims for the benefit of its progeny preserves them from decay at the same time by means of the fluid injected. In some cases, this would appear to be true, but in very many cases, of which *E. hispidarum* is one, there is no evidence for any such assumption.

5. **Life Cycle.**

The duration of the larval stage varies considerably according to the state of preservation of the host and the time occupied by the newly-hatched larvae in locating the host in the mine. There is also considerable variation in all stages with temperature.

In April, 1934, at a mean temperature of 84° F. (absolute maximum 89° F., absolute minimum 77° F.) in the room in which the parasites were kept, the mean life cycle, for individuals which fed normally on well-preserved hosts, was :—

| | | | |
|---|---|---|---|
| Incubation Period | . . . . . . . | | $1\frac{3}{4}$ days |
| 1st instar | ,, | $1\frac{1}{8}$ days | |
| 2nd ,, | ,, | $\frac{1}{2}$ day | |
| 3rd ,, | ,, | $\frac{3}{4}$ ,, | |
| 4th ,, | ,, | $2\frac{3}{8}$ days | |
| Prepupal | ,, | $\frac{7}{8}$ day | |
| Total Larval | ,, . . . . . . . | | $5\frac{5}{8}$ ,, |
| Pupal Period (to emergence from pupa, not from mine) | | | 7 ,, |
| Total Period (oviposition to emergence from pupa) | . | | $14\frac{1}{2}$ ,, |

The extremely short duration of the 2nd instar is noteworthy. The 4th instar, as estimated above, includes the period between the cessation of feeding and excretion, but does not include the prepupal period, which, however, is not a separate instar.

In July, 1933 (*i.e.* during the cool season), the corresponding total period, at a mean temperature of 76° F., was 16½ days.

6. **Natural Enemies.**

*E. hispidarum* is subject to the attacks of 4 natural enemies :—

1. *Pediculoides ventricosus.*
2. *Tetrastichus taylori.*
3. *Eupelmus* sp.
4. Eupelmid (genus near *Anastatus*).

Full accounts of the bionomics of these natural enemies and of their effects upon the *Elasmus* population are given separately, and it is only necessary here to note that *Pediculoides* and *Tetrastichus* greatly hinder the multiplication of *Elasmus*, while the 2 Eupelmids have no appreciable effect upon it.

C. *Tetrastichus taylori*, Ferr.

(Eulophidae.)

1. **Hosts.**

*Elasmus hispidarum* and very rarely *Promecotheca reichei*, one of the hosts of *E. hispidarum.*

An additional host has been provided by the introduction of *Pleurotropis parvulus* from Java, which was at once attacked.

*E. hispidarum* serves as a host not only in mines of *P. reichei* but also in those of *P. bicolor*, and is certainly the normal host.

In captivity, this insect readily attacked the introduced *Dimmockia javanica* in mines of *P. reichei*, and matured therein.

There is little doubt that there are no hosts other than those already mentioned. It will only oviposit in mines and has never been reared from any of the Dipterous or Lepidopterous mines collected in Fiji.

2. **Distribution.**

This hyperparasite is generally distributed throughout Fiji wherever its hosts occur, in both the wet and the dry zones, and since it attacks *Elasmus* in mines of *P. bicolor* as well as in those of *P. reichei* it is to be found not only in the coconut areas but also in the forests. It is invariably present in the extensive Lau outbreaks of *P. reichei.*

3. **Description of Stages.**

a. *Egg* (Plate XV). The egg is transparent, colourless, smooth and shiny. The long axis is considerably curved, and the ventral surface, when the egg is viewed laterally, is concave. The posterior end is much narrower than the anterior. The length of the egg varies from 0·27 mm. to 0·30 mm.

b. *Larva.* 1st Instar (Plate XV). There are 13 clearly defined segments in addition to the head. The greatest width is at the 2nd segment,

behind which the body tapers regularly to a point at the posterior extremity, the last segment being extremely small. The head is large and is pointed antero-ventrally, the point being a fleshy projection on which the mouth is situated. The 1st segment differs from all the others. Dorsally it is wrinkled transversely, and it is entirely without setae, while mid-ventrally it bears a minute projection, which, like a similar projection on the head, serves as a pseudopodium. Each of the remaining segments, except the last, bears a double row of minute bristles across the back, near the anterior margin of the segment, and extending down the sides but not on to the ventral surface. Otherwise the skin is smooth and shiny, and it is so transparent that the internal organs can be seen very clearly, the ventral nerve chain, cerebral mass, and gut being exceptionally readily seen. A rudimentary tracheal system (without spiracles) is already present, despite the internal habits of the parasite. The length of the 1st-instar larva, before commencement of feeding, is 0·32 mm.

The setae are lost at the first moult, and the 1st instar therefore differs strikingly from all the later instars, which are alike except in size. The number of instars was not ascertained.

Last Instar (Plate XV). The full-grown larva is similar in general appearance to those of *E. hispidarum* and *D. javanica*, and with the former it is easily confused in the field as it occurs in the same places and sometimes in the same mines. It can, however, be distinguished by its colour, size and shape.

The colour is always very pale greyish-yellow, except at the extremities which are translucent and colourless. The colour is due to the contents of the gut and is diffused through the otherwise colourless fat-body. There are 13 well-marked segments. The larva is necessarily much smaller than the average *E. hispidarum*, but its size varies greatly, according to that of the host. It is also more elongate, and when extended and viewed dorso-ventrally, it is nearly parallel-sided. The skin is transparent and very smooth and shiny. There are no setae or other external structures. Between the segments there are slight protrusions, mid-dorsally and mid-ventrally, serving as pseudopodia. These are much less prominent than in *E. hispidarum*. There are 9 pairs of spiracles, on the 2nd to the 10th segments inclusive. The mandibles are of characteristic shape and serve to distinguish this species from *E. hispidarum*. The mean length of larvae which emerge from large individuals of *E. hispidarum* is 2·52 mm. extended.

c. *Prepupa* (Plate XV). The prepupa is white, translucent, and shiny. It is readily recognised by its shape. The 1st segment is very smoothly rounded. The 2nd is much shorter, but equally smooth. The 3rd segment and all the abdominal segments are greatly wrinkled transversely. The 2nd segment (and, in the female, the abdomen) is wider than the 1st. The mouth region projects antero-ventrally as a minute papilla.

d. *Pupa* (Plate XV). The pupa is pale brown, varying from brownish-white to straw-colour. On the thorax there is a large, dark brown, patch, often clearly defined, and shaped as in the illustration. On the abdomen also there is a large, dark brown, patch mid-dorsally, but this is never clearly outlined. There is often a small, dark brown, marking on either side of the thorax, in addition to the central patch. All these markings

are very variable in extent and intensity, and the illustration shows them in their extreme form; often, especially in very small individuals such as those which result from *Pleurotropis parvulus* as host, the markings are very faint and scarcely perceptible. The cuticle is transparent, except in the regions of the markings, and is very shiny. The shape of the abdomen is characteristic. The pupa varies to an extraordinary extent in size, according to the size and species of its host. The maximum length of pupae (from *E. hispidarum*) is 2·18 mm., and the minimum length (from *P. parvulus*) is 0·95 mm.

This pupa is very readily distinguished from all other species to be found in mines in Fiji.

e. *Adult* (Plate V, f). The adult is described by Ferrière in *Stylops*, **2**: 98, 1933. The sexes are readily distinguished by their antennae.

**4. Life History.**

*Tetrastichus taylori* is an internal parasite of *Elasmus hispidarum*, and is therefore a hyperparasite of *Promecotheca reichei* and *P. bicolor*. This is its normal rôle, and its attacks upon *P. reichei* itself, as already mentioned, are of excessively rare occurrence (not more than 1 in 2,000) and often, but not always, result in the death of the parasite before reaching maturity. There is no doubt that these cases of primary parasitism by this species are wholly abnormal; nevertheless, *T. taylori*, though normally a hyperparasite, must be recognised on account of them as the only internal parasite of *Promecotheca* in Fiji, prior to the introductions from Java.

The female lays its eggs directly inside the *Elasmus* by settling upon the underside of the leaf and thrusting its ovipositor through the wall of the mine and through the cuticle of the *Elasmus* in one operation. The stages of *Elasmus* attacked are normally the 4th instar and the prepupa, most frequently the latter. The female parasite first makes a very thorough survey of the surface of the mine, tapping it incessantly with its antennae, and the act of oviposition which follows the preliminary survey occupies a considerable time and is very similar in all respects to that described for *Elasmus*. Very frequently the parasite fails to find the *Elasmus* individuals in the mine inspected, and, after a very thorough inspection, leaves the leaf without having oviposited; and not infrequently it oviposits in *Elasmus* larvae which are too small and in which its progeny cannot develop. The rare cases of primary parasitism by this species must be attributed to its occasional inability to recognise the nature of the insect in the mine; but whereas failure to recognise the age of the *Elasmus* in the mine is not uncommon, failure to discriminate between *Elasmus* and *Promecotheca* is extremely rare.

Almost invariably only one egg is laid in each host individual, and in any case only one *Tetrastichus* matures in each host. The attack of the parasite has no immediate effect upon the host except at the instant of stinging. The host is not paralysed and its development proceeds for a while quite normally. If the host is stung very early in the 4th instar, its development is usually stopped before it has excreted; if it is attacked later in the 4th instar but before it ceases feeding, it lives until after it has excreted and become a prepupa, but is usually killed as a prepupa; and if it is a prepupa when attacked, or even if it has not yet become a

prepupa but has ceased feeding for some hours, it lives until after it has pupated, and is killed as a pupa. When, as occasionally happens, the parasite attacks 3rd, or even 2nd, instar larvae, the hosts immediately become lethargic and die within 24 hours, their death resulting in the death of the contained parasites as newly-hatched larvae. As a general rule, however, it may be said that the cessation of development of the host does not occur until 2–3 days after the egg of the parasite was laid in it, and that during those days the host continues to develop normally. The time during which any one individual of *Elasmus*, in the course of its development, is liable to be attacked by *Tetrastichus* is clearly very short, for whereas the total life cycle of the host is 14–16 days, it is only liable to be attacked between the 3rd moult and pupation, that is, during a period of about 3½ days.

The egg of *T. taylori* is laid in any region of the body of the host, but always between the gut and the body-wall, where it is embedded in the fat-body. It is not attached in any way. The young larva, on leaving the egg, immediately proceeds to feed upon the body fluid. Its escape from the egg, and its movement within the host body, are facilitated by the pseudopodia and the setae already described. It is the feeding of the young larva which causes the cessation of development of the host, although no vital organs appear to be attacked at this stage. In pupae, and usually in larvae, the parasite takes up a position at the posterior end and gradually extends forwards as it grows. Eventually it devours the whole of the contents of the host body from within, so that only the skin remains, and when full grown it almost fills the host skin and is readily visible through it. Pupation takes place sometimes within the host, but more frequently outside it in the mine. When the host is a larva or prepupa, the *Tetrastichus* nearly always emerges from it to pupate. When the host is a pupa, the parasite not infrequently pupates inside it without fracturing the skin at all. The parasite larva, in emerging from the host to pupate, breaks through the skin at either the posterior or the anterior extremity, but never in the centre. The host skin, if larval, generally shrivels to a minute, unrecognisable, whisp when the parasite escapes from it, and in such cases the *Tetrastichus*, though actually a secondary parasite, might readily be assumed to be primary, and even to be *Elasmus* itself unless the differences between the two are well known. If, on the other hand, the host skin is prepupal or pupal it retains its normal form and does not shrivel, so that it is readily visible and the true status of the *Tetrastichus* is evident; moreover, in these cases, the excrement of the host is present in the mine as an additional clue.

The excrement and mode of pupation of *Tetrastichus* in the mine are the same as those for *Elasmus* and *Dimmockia*, the excrement being in the form of a lumpy, brown, mass and the pupa, which is otherwise free, being attached to it by a twisted whiteish thread which is actually the old larval skin. The time that elapses between emergence from the host and excretion is 1½–2 days, and between excretion and pupation ¾–1 day.

When there are many individuals of *Elasmus* in one mine *Tetrastichus* very rarely attacks all of them, and it therefore very frequently happens that pupae of both the primary parasite and the secondary are to be found together in the same mine.

About 12 hours after emerging from the pupa, the adult emerges from the mine in exactly the manner described for *Elasmus*. Both sexes are common, but the sex ratio was not determined. The adults are active, and are fairly strong fliers.

The adaptability of this species to its host, as regards size, is remarkable. As soon as *Pleurotropis parvulus* was introduced from Java it was attacked to a small extent by *T. taylori*, which develops quite normally in it in spite of the very much smaller size of its new host as compared with *E. hispidarum*. When attacking *P. parvulus*, *T. taylori* selects a mine containing a *Promecotheca* individual which itself contains full-grown larvae or prepupae of *P. parvulus*, and in a few of these it oviposits. The subsequent development of the secondaries is exactly as described for those in *Elasmus*, except that *T. taylori*, as a parasite of *P. parvulus*, is within the *Promecotheca* skin until it becomes adult.

In those rare instances of *T. taylori* as a primary parasite of *Promecotheca*, the stage of the host is either 1st or early 2nd instar. The unusual food appears perfectly satisfactory for the development of the parasite, but when the parasite larva has reached the maximum possible size it has never devoured all the contents of the host body; and this circumstance frequently results in its death, since, when full grown, it requires to begin to breathe air and cannot do so if surrounded by the fluid contents of the host body. Sometimes, however, it thrusts itself, preparatory to pupation, into the narrow posterior end of the host and in this position it is usually able to mature, the fluid displaced by the parasite remaining in the anterior half of the host and so permitting the skin of the posterior half to dry in such a way that there is an air space round the parasite. Subsequently, the anterior half of the host shrivels and becomes blackened and opaque, while the skin of the posterior half remains distended and semi-transparent, forming a cylindrical compartment in which the parasite pupa lies. The *Tetrastichus* never emerges from a *Promecotheca* larva to pupate, presumably because the host skin is too tough. If 2 eggs were laid in each *Promecotheca* larva, the resulting parasite larvae could mature without difficulty, since they would devour all the contents, but only one egg is laid in accordance with the normal habit of the species as a hyperparasite.

Pairing occurs at the time of emergence from the mine or at any subsequent time, and oviposition continues throughout the long life of the females when hosts are available. The adult life of females is longer than that of *E. hispidarum*. In captivity, the females usually live, when properly fed, for more than 80 days, and one lived for 117 days.

### 5. Life Cycle.

The life cycle at 84° F. (mean daily temperature) was found to be as follows :—

| | |
|---|---|
| Incubation Period . . . . . . | $1\frac{3}{4}$ days |
| Larval Period (including prepupa) . . . . | $3\frac{1}{2}$–$6\frac{3}{4}$ ,, |
| Pupal Period (to emergence of adult from pupa, not from mine) . . . . . . . | $5\frac{1}{2}$–$6\frac{1}{2}$ ,, |
| Total (oviposition to emergence) . . . . | 13–15 ,, |
| | (Mean, 14 days) |

The great variation in the larval period is due to variation in age of the hosts. In *Elasmus* larvae stung early in the 4th instar the larval development is much slower than in those stung later.

**6. Natural Enemies.**

*T. taylori* is subject to the attacks of :—

1. *Pediculoides ventricosus*
2. *Eupelmus* sp.
3. Eupelmid (genus near *Anastatus*).

Full accounts of the bionomics and economic importance of these natural enemies are given separately, and it is sufficient to note here, first, that towards the end of the dry season *P. ventricosus* destroys *T. taylori* in enormous numbers, the percentage destroyed being equal to the percentage of *Elasmus* destroyed, since the mite attacks both indiscriminately and both are equally accessible to it; and secondly, that the two Eupelmids are economically negligible as natural enemies of *T. taylori*.

## D. *Eupelmus* sp.

(Eupelmidae.)

**1. Hosts.**

This species of *Eupelmus* normally feeds upon *Elasmus hispidarum* and *Tetrastichus taylori*, but it also devours the paralysed or dead larvae of *Promecotheca* which are hosts of *E. hispidarum*.

It also attacks the introduced *Pleurotropis parvulus* as readily as its former indigenous hosts, and in captivity it was reared on *Dimmockia javanica* and also, cannibalistically, upon individuals of its own species.

There is reason to believe that this species has other hosts in no way connected with *Promecotheca*.

**2. Distribution.**

This species has only been found in the Lau group of Fiji, but within that group it is widely distributed and to be found in all extensive outbreaks of *Promecotheca*. It is always a rare insect, however, in mines of *Promecotheca*, and although in outbreaks it is present in almost every tree, it frequently cannot be found until hundreds of mines have been examined.

**3. Description of Stages.**

a. *Egg* (Plate XVI). The egg is colourless and elongate, and its chorion is smooth, very shiny, and transparent. The long axis is straight, and the posterior end is slightly narrower than the anterior. At the posterior end there is a short, very thin stalk; at the anterior end there is a long tubular process bent back upon itself and usually in contact throughout its length with the surface of the egg, but not adhering to the surface. The size varies considerably, the minimum length being 0·46 mm. and the maximum 0·54 mm.

b. *Larva.* 1st Instar (fig. 10). The head of the newly-hatched larva is large and the segmentation of the body is very distinct, there being 13 segments. The greatest width is at the 4th segment. The head

is brown, owing to chitinisation of the cuticle, but the body is translucent and colourless. In general appearance, the larva is hairy, although actually there are only 4 rows of hairs (setae)—a sub-dorsal and a lateral row on each side—each segment having one seta in each row. The hairs on the 1st segment are longer than the others, which are uniform in length. The skin on the body is rough, owing to the presence of minute raised points all over its surface, especially dorsally, but the head is smooth and shiny. The mouth is ventral, and situated on a large, prominent, papilla of circular outline. The mandibles are black. There are no pseudopodia or other appendages. The tracheal system is well developed and functional.

The width of the head is 0·12 mm.

2nd Instar (fig. 10). The 2nd and all subsequent instars differ greatly

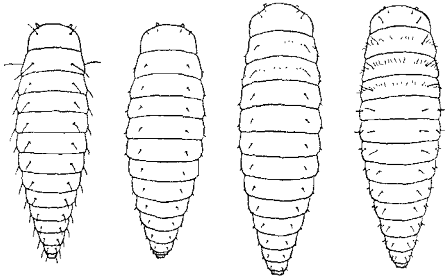



FIG. 10.—*Eupelmus* sp. a, 1st-instar larva; b, 2nd-instar larva; c, 3rd-instar larva; d, 4th-instar larva. Each at beginning of instar.

(To show outlines and chaetotaxy only.)

from the 1st in several respects, but chiefly in that after the first moult the head is colourless and the skin is absolutely smooth and shiny. In the 2nd instar, setae are present in the same positions as in the 1st, but all are now extremely short and scarcely perceptible. The width of the head is 0·21 mm.

3rd Instar (fig. 10). The 3rd instar is similar to the 2nd, except in size and in the presence of a single transverse circlet of excessively minute setae on the 1st segment and another on the 2nd. The circlets are incomplete ventrally. The other setae are in the same positions as in the previous instars, but the subdorsal setae of the first 3 segments are now considerably longer than any of the others, which are still as short, relative to the size of the body, as in the 2nd instar. The width of the head varies from 0·28 mm. to 0·31 mm., the mean being 0·29 mm.

4th Instar (fig. 10). In the 4th instar, 3 circlets of setae are present, one on each of the first 3 segments, and the setae in the circlets are now

much longer and more conspicuous. The other setae are the same, except for a slight increase in length, but there is now an additional lateral row of setae between the two previously existing rows on either side. Both the lateral rows are below the spiracles. The width of the head varies from 0·34 mm. to 0·41 mm., the mean being 0·38 mm.

5th (last) Instar (Plate XVI). In the 5th instar, especially just after the moult, the larva appears very hairy. Setae are present in exactly the same positions as in the 4th instar, but all, including the thoracic circlets, are now much longer. At the end of the instar, however, the larva appears much less hairy on account of the great increase in its size. The back is strongly arched. In each intersegmental space, dorsally, there is a fleshy, transverse, retractile protuberance functioning as a pseudopodium. There are no such protuberances ventrally. The larva has 9 pairs of spiracles situated on segments 2 to 10 inclusive. The segmentation is very distinct even when the larva is full grown. The size of the full-grown larva varies enormously according to the food-supply, but the length of the largest specimen is 4·5 mm.; the width of the head varies from 0·49 mm. to 0·54 mm., the mean being 0·51 mm.

c. *Pupa* (Plates XIV and XVI). The pupa is light yellow-brown, and opaque. It is not shiny, on account of innumerable minute pits all over its surface. On either side of the abdomen there is a row of 5 dark brown, and very shiny, spots. The very characteristic form of the pupa is clearly shown in the illustrations. When viewed laterally it is seen to be arched, and the posterior extremity is directed upwards at right angles to the long axis of the body. (The male of this species is unknown; if it exists, the male pupa is certainly without the upturned extremity, which encloses the ovipositor.) The size of the pupa varies enormously, but the length of the largest specimen is 3·7 mm.

d. *Adult* (Plate XIV). The adult is readily distinguished in the field, from all other coconut-frequenting insects, by its somewhat unusual shape, and by the rather long external ovipositor which is directed upwards from the end of the abdomen at an angle of about 30°.

### 4. Life History.

The bionomics of this insect are somewhat unusual in several respects.

The EUPELMIDAE are typically parasitic, but the present species is not a true parasite in the strictest sense of the term. As a larva it feeds externally upon larvae and pupae of *Elasmus* and *Tetrastichus* in the mines of *Promecotheca*, and when only one individual of its host is present, it necessarily feeds only upon that one, and is, in these circumstances, a true parasite, secondary or tertiary as the case may be. On the other hand, when there are several individuals of *Elasmus* or *Tetrastichus* or both in the one mine, as is often the case, it frequently moves from one to another in the course of its feeding and always attacks more than one, killing all the individuals that it attacks, but often without completely devouring any one. In such cases, it is a predator; and since, in addition, it can move about with ease and comparative rapidity, and seldom remains in one place for longer than a few hours, even when it is compelled to confine itself to one individual, it is better described as a predator within the mines of *Promecotheca* than as a parasite. The adult does not

attack mines containing healthy individuals of *Promecotheca*, and is evidently attracted only by parasites. The larva is therefore never to be found as a primary parasite. Nevertheless when the larva finds itself in a mine containing *Elasmus* larvae which have not yet completely devoured the contents of the *Promecotheca* larva which is their host, it frequently feeds, not only upon the *Elasmus*, but also upon the dead *Promecotheca*. Laboratory experiments showed that the *Eupelmus* larva, when given the opportunity, has every inclination to feed upon living *Promecotheca* larvae, although in nature it never has an opportunity to do so; but its attempts invariably failed because the *Promecotheca* succeeded, by energetic wriggling, in displacing, and often crushing, the *Eupelmus* against the wall of the mine.

The true status of this insect in the mines is very obscure until its habits are fully understood. When a *Eupelmus* oviposits in a 1st-instar mine containing a single larva of *Elasmus* or *Tetrastichus*, the host is eventually completely devoured so that no trace of it remains, not even the skin. After this has occurred there is every indication that the *Eupelmus* was a primary parasite, whereas actually it was a secondary.

Males of this species are unknown, and reproduction is wholly by parthenogenesis, which invariably resnlts in female progeny. Three successive generations were reared in the laboratory, and a large number of adults were bred out over a period of 9 months from eggs, larvae, and pupae collected in the field, but no male appeared. While it is probable that males do very rarely occur, there is no evidence whatever to suggest that their occurrence is periodic or is in any way necessary for the survival of the species.

All the true parasites and hyperparasites of *Promecotheca*, both in Java and Fiji, are attracted, when about to oviposit, by the mine rather than the insects within it. The mine is the initial stimulus; and when host individuals, which are otherwise suitable, are removed from their mines, the parasites are entirely unable to recognise them and make no attempt to attack them. The present species, however, unlike the true parasites, is strongly attracted by *Elasmus* and other larvae which have been removed from their mines, as well as by free larval or pupal skins of *Promecotheca* containing *Pleurotropis parvulus*. The mine is not the essential stimulus in these cases, and this suggests that the *Eupelmus* is not associated only with *Promecotheca*, but attacks also a variety of parasites of other insects, which are not necessarily enclosed in mines. Further evidence of the existence of other hosts, though none are definitely known, is afforded by the continuous rarity of this species in *Promecotheca* outbreaks. If it were dependent only, or even mainly, upon the parasites of *Promecotheca*, it would certainly multiply in outbreaks far more than it does, there being nothing to check it except *Pediculoides* which, while certainly capable of hindering its multiplication, cannot prevent it. We may therefore conclude that it has a great variety of hosts, which include both external and internal parasites; the former are liable to its attack at all stages in their growth, but the latter can only be attacked by it when they have devoured all the fluid contents of the host body and have commenced to breathe holopneustically.

The adult females are comparatively large and powerful, and are

strong fliers. They are occasionally to be seen in the crowns of coconut palms running rapidly over the leaves. The long external ovipositor is thrust, for the purpose of egg-laying in mines, through either the upper or the lower epidermis of the leaf, and in this respect the species differs from all the true parasites and hyperparasites, which almost always oviposit through the lower epidermis, making use of the stomata. Only one egg is laid in each mine as a rule. When the mine attacked contains *Elasmus* or *Tetrastichus* the egg is usually deposited against the wall of the mine, but sometimes it is laid directly on to the body of one of the parasite larvae. It is initially attached to the surface on which it is laid by the short stalk already described, but it frequently becomes detached, without being damaged in any way, by the activities of the other occupants of the mine. When the mine attacked contains a *Promecotheca* individual which itself contains the full-grown larvae or the prepupae of *Pleurotropis*, the *Eupelmus* pierces both the mine and the *Promecotheca* skin with its ovipositor and lays its egg amongst the *Pleurotropis* individuals but in contact at one point with the *Promecotheca* skin, to which it is usually attached by its stalk. The egg is often covered by a white, silken, web which is fairly closely woven and almost completely hides it. The web, which is attached all round its periphery to the surface on which the egg is laid, resembles a tiny cocoon and is spun by the female *Eupelmus* immediately after the act of oviposition. The construction of this relatively extensive web inside a mine by an insect outside, without any rupture of the tissues of the mine other than the minute and invisible puncture made by the ovipositor, is a remarkable achievement, and is effected by an irregular rotary movement of the body of the insect and a consequently similar movement of the extremity of the ovipositor inside the mine, the puncture in the epidermis of the leaf serving as a fulcrum. Only about 50% of the eggs, however, are covered by webs, the others being perfectly naked. Since the construction of the web is evidently a perfectly normal habit of the species, it is curious that the parasite so frequently omits to make one. The web is visible to the naked eye as a small white spot on the wall of the mine, when the latter is opened.

The host individuals are not stung or affected in any way by the *Eupelmus* when the egg is laid. The parasite usually selects for oviposition those mines which contain large larvae or prepupae of *Elasmus*, *Tetrastichus*, or *Pleurotropis*. *Elasmus*, however, is sometimes attacked in the early larval stages, but the other two parasites, being internal, cannot be directly attacked until they are full grown. Since the *Tetrastichus* larva usually emerges from its host to pupate, it is entirely unprotected against *Eupelmus* at this stage, but it is subject to attack for a shorter period in its development than *Elasmus*. Occasionally, when ovipositing in a mine containing *Pleurotropis*, *Eupelmus* lays its egg outside the dry *Promecotheca* skin which contains the parasites. In such cases, the young *Eupelmus* larva which comes out of the egg is always unable to penetrate the *Promecotheca* skin and dies of starvation. The adult *Eupelmus* seldom attacks mines containing pupae, but the larva often devours *Elasmus* or *Tetrastichus* pupae which were formed before it emerged from the egg or while it was feeding upon another larva of the same batch as those which succeeded in pupating. Pupae of *Pleurotropis*

are seldom devoured because their cuticles are too hard, and *Pleurotropis* is therefore subject to *Eupelmus* attack for only a very short period during its development.

The larva is very active. It wriggles very energetically when touched, and it crawls rapidly in the mine by means of undulations of its body. Its progress is facilitated by the hairs, which come in contact with the walls and the contents of the mine. In the 5th (last) instar, it often moves along on its back, utilising the pseudopodia, which are situated dorsally. In all instars it is exceedingly voracious, and it feeds by puncturing the skin of its hosts with its mandibles and then sucking out the body-fluid. It rarely devours any host individual completely, except when only one or two are present, as in small mines; instead, it moves from one to another, killing far more than it needs for food, and often it returns after some time to individuals on which it has fed previously. The larva can mature on a single individual of *Elasmus*, but the resulting adult is very small. To attain its maximum size it requires to devour completely at least 2 large *Elasmus* larvae or prepupae, or far more than 2 *Pleurotropis*; but it seldom attacks all the individuals present in large, 3rd-instar, mines, and consequently a pupa of *Eupelmus* is often to be found lying amongst healthy *Elasmus* pupae, or amongst healthy *Pleurotropis* pupae inside a *Promecotheca* larva or pupa.

The energetic activities and aggressive tactics of this larva contrast strikingly with the extreme sluggishness of most Chalcidoid species, including those which constitute its food. Almost invariably the larvae upon which it preys are unable to defend themselves, and die very soon after they are attacked by it, but on one occasion a *Tetrastichus* larva was observed to bend its body round and kill with its mandibles a newly-hatched *Eupelmus* larva which was about to feed upon its posterior extremity.

At each moult, the old skin remains stuck to the host larva or pupa, but it is extremely thin and delicate and can only be detected with difficulty. The head capsule of the 1st instar, however, is always readily visible after it is shed, because, being strongly chitinised, it does not shrink. All the later head capsules shrivel like the skin of the body and can seldom be detected.

The larva does not excrete until after it is full grown. The excrement, unlike that of all the true parasites associated with *Promecotheca*, is deposited in several small, brown, masses, often widely separated from one another, the larva moving about during the process.

The mean duration of the 5 larval instars, at a mean daily temperature of 85° F. was found to be :—1st instar, $1\frac{1}{2}$ days; 2nd, $\frac{1}{2}$ day; 3rd, $\frac{1}{2}$ day; 4th, 1 day; 5th (to cessation of feeding), 3 days. The time that elapsed between the cessation of feeding and pupation varied from $2\frac{3}{4}$ to $3\frac{1}{2}$ days at the same temperature, and excretion, which is a long process and occupies about 12 hours, occurred at approximately the middle of this period. The extremely short duration of the 2nd and 3rd instars is noteworthy.

The pupa is attached to one of the masses of excrement or to the wall of the mine by a thin thread, which is the old larval skin, and which is similar to that of the true parasites already described except that it is

hairy throughout its length, the larval hairs remaining attached when the skin is shed. The pupa is not enclosed in any sort of cocoon, but is quite naked, and it is not attached in any way except by the larval skin.

After emerging from the pupal skin, the adult rests for about 24 hours within the mine. It then emerges, usually through the upper epidermis of the leaf, by biting a neat circular hole. A hole made by a large individual is much larger than that of any of the true parasites, but a hole made by a smaller individual cannot be distinguished from that of *Elasmus* or *Tetrastichus*, although it is much larger than that of *Pleurotropis*.

The adult life covers about 2 months, judging from individuals kept separately in glass tubes and provided regularly with suitable food. Oviposition proceeds slowly throughout life.

5. **Life Cycle.**

In the hot season, at a mean temperature of 85° F. (max. 93° F., min. 79° F.), the life cycle was found to be as follows :—

| | | |
|---|---|---|
| Incubation Period | $1\frac{3}{8}$ | days (mean) |
| Larval Period (including prepupa) | $9\frac{1}{4}$ | ,, ,, |
| Pupal Period (to emergence from pupa, not from mine) | $7\frac{3}{4}$ | ,, ,, |
| Total (oviposition to emergence) | $18\frac{1}{4}$ | ,, ,, |

These figures only apply to individuals constantly provided with an ample supply of suitable food. When the food supply is limited the larval period is protracted, sometimes to as long as $12\frac{1}{2}$ days. The pupal period is nearly constant so long as the temperature remains constant; in the cool season, at a mean temperature of 79° F., the mean pupal period was 9 days.

6. **Natural Enemies.**

*Eupelmus* sp. is subject to the attack of *Pediculoides ventricosus* only.

### E. Eupelmid (Genus near *Anastatus*).

This species is extraordinarily similar to the other Eupelmid, just described, in nearly all respects. The notes already given concerning the hosts, distribution, natural enemies, and economic importance, of the latter species apply in every particular to the present species, which exhibits also the same degree of rarity and has exactly the same status within the mines. The early stages can be distinguished, but only with difficulty, and the habits in all stages are almost identical. It is therefore only necessary to point out here the few morphological and bionomic differences which do exist.

1. **Description of Stages.**

a. *Egg* (Plate XVI). The egg is very similar to that of the other Eupelmid, but is always smaller and less elongate, while the recurved appendage is shorter, relative to the length of the egg. The length varies from 0·39 mm. to 0·42 mm.

b. *Larva*. 1st Instar (Plate XVI). The 1st-instar larva differs from that of the previous species only in that the hairs are noticeably longer and those of the 11th segment are longer than any others on the abdomen.

2nd, 3rd, 4th, and 5th Instars. The larvae of the two species are identical in these instars except in the lengths of the hairs, which are always longer in the present species.

The mean widths of the head-capsules in the 5 instars are :—0·10, 0·15, 0·27, 0·35, and 0·47 mm., respectively. The head is therefore consistently smaller than in the other species, but the differences are not great enough to be regarded as reliable specific characters. They are, however, invaluable as means of distinguishing the instars; the hairs being difficult to see when they are short as in the 2nd, 3rd, and 4th instars.

c. *Pupa* (Plates XIV and XVI). The pupae of the two species, though very similar in general appearance, are readily distinguishable. In the present species, the end of the abdomen is not turned upwards, and there are only 4 shiny, dark brown, spots on either side of the abdomen. In front of the 4 spots on either side there is a depression, which, at a glance, often looks like a fifth spot, but it is not pigmented and its surface is not shiny. There is no sexual dimorphism in the pupa. The shape varies to some extent, the abdomen often being narrower than the thorax, but this is not a sex character. The size varies very greatly, according to the food-supply of the larva. The mean length of 12 specimens was 2·31 mm., and the maximum length was 2·60 mm.

d. *Adult* (Plate XIV). Since no male occurs in *Eupelmus* sp., males can at once be attributed to the present species. The females are distinguishable at once by their shape, as well as by the fact that the present species has smoky wings and a short ovipositor.

### 2. Life History.

The most important bionomic difference between the two species is that whereas in *Eupelmus* sp. no male is known and reproduction is parthenogenetic, in this other Eupelmid males occur as frequently as females and sexual reproduction is the rule. Pairing takes place on the day of emergence from the mines, or at any subsequent time. On many occasions attempts were made to cross-pair the two species, but in no circumstances was the male in the least attracted by the female of *Eupelmus* sp., although it always paired immediately with its own kind. The present species is even more active and lively than the last. The adults crawl over the leaves with characteristic rapid, darting, movements, and they take off for flight with a jump that is so sudden that they vanish completely and cannot be followed with the eye. The duration of the adult life of the female of this species is the same as for *Eupelmus* sp. The male dies 1 or 2 days after pairing, but it lives for approximately 2 weeks if it has not paired.

In all other respects the habits of the two species in all stages are identical. It is particularly remarkable that the present species, like the last, often, but by no means invariably, covers its eggs in the mines with webs. The rates of growth of the larvae are approximately the same,

but the durations of the 5 instars were not determined with accuracy for the present species.

### 3. Life Cycle.

In the hot season, the life cycle was found to be as follows :—

| | |
|---|---|
| Incubation Period . . . . . . . | $1\frac{1}{2}$ days |
| Larval Period (including prepupa) . . . . | $8\frac{1}{2}$ ,, |
| Pupal Period (to emergence from pupa, not from mine) . . . . . . . . | 9 ,, |
| Total . . . . . . . . . | 19–21 ,, |

The pupal period is consistently longer, at a given temperature, than that of *Eupelmus* sp. In the cool season the total period of the life cycle is longer by about 4 days.

## F. Pediculoides ventricosus, Newp.

(Acarina—Tarsonemidae.)

### 1. Hosts.

*P. ventricosus*, which is a parasitic mite, has a great variety of hosts, including man. Its recorded insect hosts include Lepidoptera, Coleoptera, Diptera, and Hymenoptera. Very little is known of its hosts in Fiji, and it has been recorded only from *Levuana iridescens*, *Promecotheca reichei*, and the parasites and hyperparasites of the latter (including the introduced internal parasite, *P. parvulus*). There is, however, no doubt that it has very many hosts in Fiji, as elsewhere: and these most probably include several species which feed in stored products (grain, flour, etc.), and which are known to be hosts in other countries. In coconut trees, no hosts other than those mentioned above are known, but in the writer's opinion the mite is certain to attack the three species of *Batrachedra*, as well as other Tineids, which are common in coconut trees. It is also cannibalistic.

### 2. Distribution.

The distribution of *P. ventricosus* is almost world-wide. Since its known hosts include insects such as *Sititroga cerealella* and Bruchids, it is very readily carried everywhere in stored products. It certainly is not indigenous in Fiji.

In Fiji, it is very widely distributed, and it is present on all the larger islands and many small ones. It was first recorded in Fiji by A. G. Carment in 1921, as a parasite of *L. iridescens*, but there is every reason to believe that it reached Fiji long before that. As a parasite of *P. reichei*, it is invariably present in every outbreak in the Lau Group; in other parts of Fiji it is nearly always, but not invariably, present in outbreaks.

### 3. Life History.

*P. ventricosus* is an external parasite of the larvae, pupae, and occasionally the adults, of many species of insects. It feeds by penetrating the integument of its victim with its mouth-parts and sucking out the body-fluid. It is almost wholly restricted to insects that live in partial or

complete confinement by mining, boring, making silken tunnels, or making cocoons. It is further greatly restricted in its choice of hosts by the degree of hardness of their integuments, being able to feed only upon those whose integuments are soft and thin. Laboratory observations showed that many insects, which are ordinarily immune from its attack on account of the hardness of their skins, can be attacked and killed by it just after each moult, and before the integument hardens. Free-living adult insects never succumb to its attack because of their activity and the ease and frequency with which they clean their bodies, but newly-emerged adults, whose integuments are still soft, are liable to be destroyed by it in their cocoons or mines. Free-living larvae, such as caterpillars which feed exposed on leaves, are rarely attacked by it, on account of their activity and their relatively strong integuments, but the same individuals may succumb to it later as pupae in cocoons if the pupal integument is soft. The mite is extremely minute when it commences to feed, and very few of the insects which it attacks are aware of its presence when it is crawling over them. Their degree of immunity therefore depends largely upon the texture of their integuments and upon the frequency and rapidity with which they normally move.

*P. ventricosus* can become abundant only when the individuals of its host are crowded together. The massed pupae of *Levuana iridescens*, prior to the control of that insect by *Ptychomyia remota*, were eminently suitable for its attack; and the crowded individuals of *S. cerealella* in badly infested grain, and of *P. reichei* in coconut trees in severe outbreaks, are similarly suitable. The mite, when searching for food, is remarkably active, and when its size is considered the speed of its movement and the distance it can travel are surprisingly great; nevertheless, the distance is actually small and the duration of its roving life is short, so that when the host individuals are widely separated, as in the case of *P. reichei* larvae on different leaves, the newly-born mites cannot easily find them. Consequently, the percentage destruction by the mite is always negligible or nil when the host individuals are widely separated, but often reaches 100% when they are crowded together in otherwise identical conditions. Wherever *P. reichei* is in non-outbreak condition, it usually is not attacked at all by the mite, and so long as it remains in that condition (for a period of several years in some localities), it cannot be included in the list of functioning hosts for the localities in question; but as soon as *P. reichei* multiplies sufficiently to constitute an outbreak, it becomes the principal host of the mite.

*P. reichei* is protected to a considerable extent by its mine from the attacks of *P. ventricosus*. The mites cannot bore their way through the stomata of the leaf or penetrate intact leaf tissues, living or dead, in any manner whatsoever. They can enter the mines only at the places at which the *Promecotheca* larvae themselves entered, namely, the small slits in the lower epidermis, covered by the egg capsules. The mites often wander for hours over leaves containing mines and fail to find the slits. They are unable, except by chance, to follow the course of a mine until they arrive at the egg capsule. Consequently, when only one or two mites are on a leaflet containing a mine, the *Promecotheca* individual often remains unattacked, but when the mites are more abundant one invariably

finds the slit by chance sooner or later, and having found it, always enters.

Except for the initial protection afforded by the mine, which is a greater protection than the habitats of most other hosts of the mite afford, *P. reichei* is particularly well suited for the mite's attack. Throughout the larval pupal, and early adult stages *P. reichei* is confined within the mine, so that its movement is very restricted, and in all these stages its integument is soft enough to be penetrated by the mouth-parts of the mite. In the egg stage it is very rarely attacked, because the mite cannot penetrate beneath the egg-capsule, which adheres very closely and tightly, all round its edge and all over its flat surface, to the leaf. When the egg hatches, however, and the larva begins mining while still beneath the capsule, the anterior edge of the capsule is loosened, and subsequently that part of the chorion of the egg which is in contact with the leaf dries and wrinkles to some extent after the larva has made a slit in it and entered the leaf. From this time onwards the mite can gain access to the mine by penetrating beneath the capsule, and *P. reichei* is liable to be attacked from the moment it hatches until shortly after it emerges as an adult from the pupa, when the adult integument becomes too hard.

The development of *P. ventricosus* has been described by many authors, including R. W. Paine who studied it in Fiji with *L. iridescens* as host. We shall therefore confine our attention here to its development on *P. reichei* and on the parasites of the latter.

The eggs of *P. ventricosus* hatch in the parent uterus, and the progeny reach sexual maturity before birth. Pairing occurs at birth or very soon afterwards, and each newly-born female then wanders off in search of food. If food is available, it begins feeding at once, but if not, it can live and wander for several days without food. The maximum possible duration of life without food is 4 days, but the majority die much sooner. Having once penetrated to the interior of a mine, the mite attacks the first living thing that it finds. This may be a larva, pupa, or newly-emerged adult of *P. reichei* itself or of any of its primary or secondary parasites. All are equally accessible to it and are equally readily attacked by it.

*P. ventricosus* takes up its position for feeding on any part of the body of the host, but if the host is a *Promecotheca* larva, it shows preference for the intersegmental regions or the sides, where it cannot be displaced against the mine when the host moves. If the host is a *Promecotheca* pupa, the mite is more restricted in its choice of position, except when the pupa is newly formed, because the back and the ventral surface of the thorax are too strongly chitinised. The preferred position on a pupa is at the ventral junction of the thorax and the abdomen, beneath the overlapping sheaths of the appendages. In this position the mite is invisible when it commences to feed, but as it grows it can be seen projecting beyond the appendages. Very often, however, the mite avails itself of the sutures on the ventral surface of the thorax, and any part of the abdomen is liable to be attacked by it. When it is attacking newly-emerged adult beetles it usually penetrates beneath the elytra and wings and takes up its position on the dorsal surface of the abdomen, where the integument is thinner than elsewhere, but the sutures in all parts of the

body are liable to its attack. When attacking larvae or pupae of *Elasmus*, *Tetrastichus*, *Pleurotropis*, or *Anastatus*, it can penetrate the integument in almost any region of the body.

Visible growth commences about an hour after the mite has begun to feed. The body as a whole does not grow at all, growth being restricted to the posterior end of the body, which swells and extends backwards so that it is first ovoid and then spherical. The extreme posterior tip of the body does not grow, but persists as a tiny papilla, with a pair of bristles projecting from it, on the posterior surface of the swelling (Plate XVII). The swelling enlarges very rapidly and ultimately attains an astonishing size, so that the original, non-swollen, body of the mite is merely a tiny projection from a relatively enormous sphere, like a match projecting from a tennis ball (Plate XVII). When the sphere has reached its maximum size its diameter is approximately 36 times the original width of the posterior portion of the body from which it has been derived, while its volume is no less than 40,000 times that of the latter (approximately). This extent of growth is the more remarkable in view of the fact that the mite is adult at birth, before it commences to grow. The size ultimately attained varies greatly, according to the quantity and quality of the available food. Thus, if a single mite feeds on a 1st-instar larva of *Promecotheca*, it usually attains a size which approximates to the maximum, but if 2 mites feed simultaneously on a 1st-instar larva, both mature, but are small when full grown. Similarly, if the host commences to decay before the mite ceases feeding, the mite usually matures but is unusually small when full grown.

The host always dies as a result of the puncturing of its integument by the mite, and there is no doubt that some toxic substance is injected. The death of the host invariably occurs withiu 24 hours from the time when the mite punctured it, and often much sooner. Normally each mite feeds on only one host individual and continues feeding at the same puncture throughout its development; but not infrequently, when already considerably swollen, it moves to a different position on the same host and resumes feeding in the new position, and occasionally, after feeding for a short time on a larva of one of the Hymenopterous parasites, it moves to a neighbouring larva of the same or another species and continues feeding on the new host. The host, if small, often shrivels and dries up before the mite is full grown, and large hosts often decay, but as a rule the host, regardless of species or size, remains in a good state of preservation and retains its normal appearance until long after the mite which caused its death is full grown. The shrivelling and decaying of the host, except when it is a 1st-instar larva, rarely cause premature death of the mite, which, in these circumstances, usually matures but is undersized. As the mite swells, its capacity for movement steadily decreases, until, when it attains its maximum size, it is almost incapable of movement on account of the relatively minute size of the non-swollen part of its body, which bears the legs. When full grown, however, it is capable of slight movement, if disturbed, to the extent of rotating the sphere slightly about the axis which passes through the point of contact with the host, but normally no such movement occurs.

*P. ventricosus* very commonly attacks the young larva just after it

leaves the egg and when only its anterior half is in the leaf. The mite enters the egg-capsule through the slit in the chorion, pushing past the larva, and then attacks the posterior extremity of the larva. Its growth then takes place wholly within the egg-capsule, and the host is killed when it has only just begun to feed and its mine scarcely shows at the anterior edge of the egg. In such cases, and also in older 1st-instar mines, the host often shrivels and dries very soon after it dies and the mite does not mature. Very often, in the field, large numbers of mines which ceased to grow when they were very small are noticeable towards the end of each generation when the majority of mines are large; when opened, they are found to contain no indication of the cause of death of their normal occupants, but actually the cause in almost every case is a mite, the minute remains of which have vanished amongst the other debris of the mine. This is readily ascertained if a daily inspection of the young mines is made from the time when the eggs begin to hatch, but at no other time is it possible, in most cases, to ascertain the cause of death.*

While the mite is feeding and growing, its eggs and young develop within its body. By the time the parent is full grown and ceases feeding, its progeny are usually adult. The birth of the first of the offspring normally occurs about 24 hours after the parent has ceased to feed. The offspring are born singly and irregularly, and the production of them proceeds for a period varying from 6 days to more than 2 weeks, the mean being about 10 days. The number produced per day varies very greatly. The average total number of offspring produced by a normally healthy mite which has fed upon *P. reichei* is approximately 90, but in exceptional cases the total is nearly 200. The sexes occur in very unequal numbers, the males being only 4%. No wholly female brood was ever observed by the writer, however, and the majority of broods included either 3 or 4 males. The first offspring produced is usually, but not invariably, a male; and in the writer's experience, there is always a male in the first three. The males are very lethargic and do not feed. They nearly always stay upon the sphere from which they were born. They remain motionless for long periods near the genital aperture of the parent sphere, waiting for the females to be born, and from time to time they wander slowly over it. Pairing occurs as soon as each female is born, or soon afterwards, and after pairing the newly-impregnated female leaves the parent sphere and the male remains. The sphere, which is at first tightly distended, shrinks and wrinkles more and more as the offspring are produced. Parthenogenesis, resulting in an arrhenotokous generation, can take place in the laboratory, but in the field it is certainly an excessively rare occurrence. No evidence of it was ever found in the field by the writer.

A single pupa or large larva of *P. reichei* can support a very large number of *P. ventricosus*. As a rule, the host is initially attacked and killed by a single mite, but the feeding of one mite does not reduce the host contents appreciably, if the host is large, and consequently the earlier

* When the trees are suffering from extreme drought, many 1st-instar larvae die through the abnormally rapid death and hardening of the tissues immediately in front of their mines. In all other circumstances, however, the death of young larvae in large numbers is due to mites.

individuals of the first generation of offspring have an abundant supply of food readily available, and they take full advantage of it. A partial second generation is usually possible on the same host. The dead host becomes absolutely covered with mites of all ages and sizes, so that it is almost wholly hidden by them and looks like a bunch of tiny balloons (Plate XIV, a). Many of the mites are later unable to obtain an adequate food supply, and are undersized and of a dirty brown colour, while their reproductive capacity is greatly reduced. From this mass, a constant stream of newly-born mites issues, at the rate of hundreds per day, and large numbers escape from the mine, under the egg-capsule, and spread over the leaves to infect other mines. At the time when the mites reach their maximum abundance in outbreaks of *P. reichei* there are approximately five million in every coconut tree, and the great majority die from lack of food. On account of the enormous excess of mites present on these occasions, every single host individual in the larval and pupal stages is destroyed, only eggs and active adults escaping. The extremely rapid multiplication of the mite and its minute size make it a great menace in the laboratory, and every precaution must be taken to control it by frequent sterilisation of all glass and other containers which are employed for the experimental breeding of any of its hosts.

Sexual dimorphism is very marked, even before the female begins to swell (Plate XVII). The male is broadly oval in outline, very convex dorsally, translucent, and pale yellow in colour. The dorsal surface bears 4 pairs of bristles, as shown in the figure. The 1st and 4th legs terminate in a claw, and the 2nd and 3rd in a sucker. The length of the body is 0·15 mm.

The newly-born female differs greatly from the male in shape, though similar in translucency and colour. It is much more elongate, and is widest just behind the middle, tapering anteriorly and posteriorly. The dorsal surface bears 6 pairs of bristles in the positions shown in the figure. The internal organs, notably the 2 main tracheae and the ovary, are readily visible through the transparent integument. The first leg terminates in a small claw. The other 3 legs terminate in a pair of minute claws and a sucker. A long, twisted, bristle projects backwards from the tarsus of the 4th leg. A small vesicle projects, on either side of the body, between the 1st and 2nd legs. The length of the body is 0·22 mm.

The gravid female is simply a relatively enormous sphere, which is derived from the hind end of the body of the newly-born female, and from which the remainder of the body of the latter projects unchanged in form. The integument of the sphere is absolutely smooth, very shiny, very thin, and of a glassy transparency. The internal organs are very clearly visible. The general colour of the sphere, for normal individuals, is pale yellow, with asymmetrical and irregular whiteish patches which are the hepatic sacs and fat-body; but if the food is not entirely suitable in quantity or quality the general colour is brown. The maximum diameter of the sphere for individuals fed upon *P. reichei* was 1·02 mm. and the mean was 0·86 mm., but Paine has recorded a maximum diameter of 1·22 mm. in Fiji for individuals fed upon *L. iridescens*.

The male and unimpregnated female are only just visible to the naked

eye. The gravid female is readily visible and a conspicuous object on its host.

### 4. Life Cycle.

The whole life cycle, from the birth of the individual to the birth of the first of its progeny, was found to cover 6 days at Nabavatu at a mean temperature of 80·5° F. (max. 88° F., min. 76° F.) and a mean humidity of 74%. This is less by 2 days than the mean period (8 days) recorded by Paine at a mean temperature of 81·5° F. (mean max. 85° F., mean min. 78° F.) and with *L. iridescens* as host. It is unlikely that the difference was due to the different hosts, and it must therefore be attributed to the difference in temperature, although the means only differ by 1° F. Wildermouth found that the development is most rapid between 70° and 80° F.

Since the production of offspring commences when the parent is 6 days old and ends when it is 12 days old at the earliest and 20 days old at the latest, the average duration of one generation, if all the individuals of one brood are considered, is $\frac{1}{2}\left(\frac{6+12}{2}+\frac{6+20}{2}\right)$ days, which is 11 days.

It was found at Nabavatu that the rate of development was nearly constant, in the conditions cited above, provided the host remained normal in colour, its colour indicating its state of preservation. If the host decayed and became discoloured the life cycle nearly always covered a much longer period, extending in one instauce to 10 days.

### 5. Means of Spread.

*P. ventricosus* is spread by wind, and by insects, birds, bats, and man.

The constant lashing of the coconut leaves by the wind, particularly the strong and continuous trade wind, causes many mites to be dislodged and many mines containing mites to be ripped open. The dislodging of the mites has often been witnessed by the writer, and they are undoubtedly carried long distances by the wind, like dust. It should, however, be noted that no actual tests were made to ascertain the distances through which the mites could be carried.

The mites are frequently to be seen crawling over the bodies of Coccinellid beetles, *P. reichei* adults, and other insects which settle in the coconut trees, and are certainly carried from tree to tree in this way. It also seems certain, though not proved, that birds must be a most important factor in spreading *P. ventricosus*, since their feathers, in brushing the leaves, must collect large numbers of the mites. Bats may be assumed to carry them similarly.

The transport of the mites from island to island is effected mainly by ships. Baskets made of coconut leaves are in general use throughout the islands, and in these baskets, mines of *P. reichei* containing *P. ventricosus* are commonly to be found in boats of all kinds, especially in the Lau group. The mite also has many hosts in stored products, such as grain, flour, and probably copra, and is therefore likely to be present in the cargoes of most ships.

### 6. Effect of Rainfall and other Climatic Factors on *P. ventricosus.*

Rainfall is a factor of paramount importance in connection with the behaviour of *P. ventricosus* in bulk in the field. At the beginning of the dry season in every year and in every island throughout Fiji, *P. ventricosus* is exceedingly rare in the field; in outbreaks it is always present, and it can always be found in mines of *P. reichei* if a prolonged search is made, but it is absolutely negligible at this time of the year as an enemy of *P. reichei*. As the dry season proceeds, however, the mite becomes increasingly common, until, at the end of the season (*i.e.* in September and October) it is extremely abundant if *P. reichei* is itself plentiful. Isolated showers in the dry season, even if heavy, have no apparent effect upon the mite. When the wet season begins, however, the mite disappears. If, after a long period of drought, rain falls heavily and continuously for 2 or more days, the disappearance of the mite is immediate and almost complete. On the other hand, if the rain falls for several days, but only in light intermittent showers, with sunny intervals between them, its disappearance is much more gradual, but equally extensive ultimately. It remains rare throughout the wet season.

Rain affects the mites adversely in three different ways. Firstly, their progress over the leaves is greatly hampered during rain, and for a few hours afterwards, by the film of moisture which covers the leaves, and if the leaves become wet on both sides, as in driving rain, the mobility of the mites is reduced almost to nil. Secondly, heavy, driviug, rain simply washes them off the leaves; experiments showed that they cannot grip firmly on a wet leaf surface, and are readily displaced by a drop of water or running water. Lastly, heavy rains, or light continuous rains, cause the mines to fill with water, particularly when they are small, and the inner surfaces of the mines remain very wet for some hours after most of the water has evaporated. This is the most important factor. It results in wholesale drowning of mites of all ages in the mines, and causes premature decay of their hosts.

The importance of rainfall in causing the almost complete disappearance of *P. ventricosus* annually, and always at approximately the same time of the year, cannot be too strongly emphasised. Its effect in outbreaks is fully discussed in a later section.

No other climatic factors are of great importance in this connection. The influence of wind in spreading the mite has already been noted. The seasonal temperature changes, which are considerable and cause marked changes in the rates of development of *P. reichei* itself and of all the Hymenopterous parasites, do not affect the mite greatly. The mean temperature in the hottest months is about 82° F. and in the coolest months is about 73° F., and the rate of development of the mite is approximately constant between 70° and 80° F. There appears, however, to be a slight reduction in its rate of development in the hot season, and in this respect the mite differs from *P. reichei* and its Hymenopterous parasites.

## G. Ants.

The minute ant, *Monomorium floricola*, Jerd., is commonly to be seen devouring eggs of *P. reichei* and is to be found inside the mines feeding

upon the larvae, pupae, and newly-emerged adults. It frequently nests inside the mines.

When attacking an egg, it usually bites a large irregular hole in the edge of the capsule (Plate V, b), and sometimes removes half the capsule. The holes are not always at the edge, however, and may be in the same positions as those of *O. utilis*. They are invariably very easy to distinguish from the latter on account of their much larger size and their irregular outline. Each egg is normally attacked by one ant only. The ant removes the contents of the egg completely and devours parasitised eggs as readily as healthy ones.

When attacking a mine, the ant bites a hole in the wall of the mine, usually in the lower surface of the leaf, but sometimes in the upper surface. The hole, which may be in any section of the mine, is usually extremely small—much smaller than the hole which the ant makes in an egg, and also much smaller than the hole made by *Elasmus*. The hole is ragged in outline, and very often one or two minute strands of tissue remain across it. Having entered the mine, the ant immediately attacks the *P. reichei* individual inside it, and as a rule it is followed by many other ants, in which case the normal occupant of the mine is rapidly devoured. The ant devours the primary and secondary parasites of *P. reichei* as well as *P. reichei* itself.

This ant is a very general predator, but the conditions that prevail in outbreaks of *P. reichei* are peculiarly well suited to its requirements, and in these circumstances it probably eats little else. Food is abundant on every leaf, and the mines afford suitably sheltered sites for nesting purposes.

Two other species of ant attack *P. reichei* occasionally, but are of no importance.

### H. Lizards.*

Lizards of more than one species are very common in coconut trees in Fiji, as in most other tropical countries. They do not often attack the larvae and pupae of *P. reichei*, but they occasionally do so in periods of drought, and having once begun to feed upon them they continue with remarkable thoroughness. The stages most frequently attacked are large larvae and pupae. Eggs and 1st-instar larvae are never attacked. The fact that lizards rarely attack the larvae and pupae, but feed on them very extensively having once begun to do so, suggests that the larvae and pupae are ordinarily immune from attack through being hidden within the leaves, the lizards failing to discover this very prolific source of food which is constantly available, though invisible. In the dry season, insects generally are scarce in Fiji, and this would account for the observation that lizards attack the larvae and pupae most frequently in dry weather.

The symptoms of the attack of lizards upon the mines are very characteristic and are always the same in all mines and all localities.

* Lizards were never actually observed to attack *P. reichei* mines, but there appears to be nothing else which would account for the damage to the mines described here. It certainly is not due to birds. Rats and bats are plentiful in coconut trees, but it is most improbable that they would attack larvae and pupae of *P. reichei*.

No actual hole is made in the mines, but there are always 2 parallel slits about an inch long and a tenth of an inch apart in the upper epidermis. The slits are usually in that section of the mine in which the larva or pupa was situated; that is to say, in a larval mine they are near the broad end and in a pupal mine they are nearer the narrower end. The means by which the slits are made and the extraction of the occupant of the mine were never actually observed. The upper wall of the mine, if pulled, always tears in a straight line, and it seems probable that the lizard grips the upper wall with its mouth so as to make a fold and then rips it by pulling.

Lizards have occasionally been observed to stalk and attack the adult beetles, and it is most probable that this is a common occurrence. The difficulty of observing lizards in the trees would account for the fact that they are not more frequently seen to attack beetles. The beetles, however, are protected to a large extent from lizard attack by their habit of dropping from the leaves at the slightest disturbance.

### I. Coccinellids.

Coccinellids do not attack any stage of *P. reichei*, but they frequently utilise the mines for oviposition purposes. They do not make holes in the mines, or damage them in any way, but they use the holes made by *Elasmus* and ants. They insert their ovipositors through these holes and lay their eggs inside the mine, close to the holes. The number of eggs per mine is usually 2, but varies from 1 to 4. When the eggs hatch, the young larvae immediately leave the mines, and from this time onwards they are not in any way associated with *Promecotheca*. The frequency with which Coccinellid eggs are found within the mines leads to the impression that Coccinellid larvae and adults commonly feed upon *P. reichei*, but this is entirely erroneous. Laboratory tests showed that neither the larvae which result from eggs found in mines nor the adult Coccinellids found in the coconut trees would attack eggs or mines of *P. reichei* and would very rarely attack larvae removed from their mines, and in the field no indication of the attack of Coccinellids was ever seen.

The eggs found in the mines belong to at least 2 species, but no attempt to rear the adults was made, and their identity therefore remains unknown. *Anisorcus affinis*, Crotch., and *Chilocorus nigritis*, F., are two species of Coccinellids which are often very common in coconut trees in Fiji, both in the presence and in the absence of *P. reichei*, and it is very probable that it is these species that oviposit in the mines.

### J. Mites (other than *P. ventricosus*).

A mite, *Tyroglyphus* sp., occasionally attacks 1st-instar larvae of *P. reichei*, but it appears never to attack older larvae or pupae—presumably because they are able, by their activity and strength, to frustrate it. It is essentially an enemy of lethargic and comparatively helpless insects, and is much more common as an enemy of *Elasmus hispidarum* than of 1st-instar *P. reichei*. It enters the mines through the slit under the egg-capsule, and grows and oviposits in the mines. In a mine con-

taining several larvae or pupae of *Elasmus* there is usually sufficient food for a partial second generation of mites, and all the *Elasmus* individuals are eventually killed. 1st-instar larvae of *P. reichei* usually serve as food only for the one mite which enters the mine initially because they dry up rapidly when they are killed. When there is no food left in the mine the young mites leave through the slit. As it grows, the mite moves from place to place within the mine, and it often feeds on more than one individual of *Elasmus* although it does not devour any one completely. It remains active throughout its life, unlike *P. ventricosus*. For these reasons, it must be regarded as a predator, not as a parasite.

This mite became a much more frequent occupant of the mines as a result of the introduction of *P. parvulus* from Java in 1933. It was evident that *P. parvulus* was much better suited to its habits than *Elasmus* or *P. reichei*. Prior to 1933, the mite was eldom fosund in the mines and was very local. Certainly it was of no economic importance. It can undoubtedly feed on a great variety of insects, mostly parasitic, and its habits are such that it can feed and breed more readily when the individuals which constitute its food are small and numerous, and are crowded together, than when they are comparatively large and isolated.

At least two other species of mite are present commonly in the mines, but these are scavengers only.

### K. An Attid Spider (*Ascyltus pterygodes*, Koch).

This spider is very common in coconut trees throughout Fiji. It attacks only adults of *P. reichei*, and these only occasionally. It feeds on a great variety of insects, but its food consists mainly of soft-bodied insects and rarely includes Coleoptera. In captivity, however, it will eat almost any insect which is fully exposed to its attack. It destroyed *P. reichei* adults very readily in large breeding-cages, but in the field it was observed to attack them on two occasions only. It eats larvae and pupae of *P. reichei* if these are removed from their mines, but never attacks them in their mines.

### L. "Parasite A." *

In March, 1932, R. W. Paine found cocoons of an unknown insect, probably an Ichneumonid or Braconid, in 2nd- and 3rd-instar mines of *P. reichei* collected at Savu Savu Point, Vanua Levu. The cocoons were empty, and the parasite has never been found since, so that its identity remains unknown. It is certainly very rare as a parasite of *P. reichei*, and is almost certainly absent from the Lau Group, where many thousands of mines from many localities have been examined without any trace of it being found. The cocoons were large, approximating in size to the sizes of the *Promecotheca* larvae on which the parasites must have fed, and there was one cocoon per mine; in colour they were greyish, in shape oblong, and they were compactly but somewhat flimsily woven. They were spun against the walls of the mines, and were incomplete between the edges which were in contact with the mines. In every case the

* The writer is indebted to Mr. R. W. Paine for providing information concerning this parasite.

remains of the dead host were found at the end of the mine where it had fed; and little was left but the head-capsule, which proves that the parasite is external, as the dried skins of larvae attacked by internal parasites persist for many months. There were small circular emergence holes in many of the mines, the parasite which made them having bitten straight through cocoon and epidermis. These holes were only slightly larger than the holes made by large *Elasmus*, and seemed very small in view of the size of the cocoons. Their size suggests that they may have been made by secondary parasites which had fed inside the cocoons upon the parasites which made the cocoons. Two dead parasite larvae were found at the same time in two other mines lying against the shrivelled remains of the *P. reichei* larvae. They were too large for *Elasmus* larvae and were almost certainly of this species.

## M. A Fungus.

In the wet season, adults of *P. reichei* are killed in small numbers by an undetermined fungus, which attaches them to the leaves and eventually grows over them and fructifies so that they resemble small pieces of cotton-wool. In the Philippines, similar entomogenous fungi (*Beauveria* spp.) have been found attacking the allied *Promecotheca cumingi*, Baly. In Fiji this occurrence is very rare, and no indication of an epidemic of the fungus has ever been found.

# IV. *PROMECOTHECA REICHEI* AS AN INSECT OF ECONOMIC IMPORTANCE.

## A. The Nature, Extent, and Results of the Damage done to the Trees.

### 1. General Nature of Damage.

*P. reichei* is a pest of coconut palms only. It attacks the leaves, and no other part of the tree. The direct damage is of two kinds : the adults feed externally on the undersides of the distal thirds or halves of the leaflets, and to a less extent on the other parts of the leaflets, and cause the distal thirds or halves to die outright and curl over towards the ground ; and the larvae feed by mining in the more proximal parts of the leaflets and greatly reduce the functioning area of the leaf surface without, however, causing the immediate death, except in extreme cases, of the tissue between their mines. The adults and larvae together cause great weakening of the trees by reducing the leaf surface, and there is consequently a great reduction, and often a complete cessation, in the production of nuts, and therefore in the output of copra.

The ravages of *P. reichei* are sporadic and intermittent, not uniform and continuous. As a pest, it occurs in outbreaks, and these are often of extreme severity and cover wide areas of country. Within an outbreak area all the trees are attacked.

### 2. Damage Done by Adult Beetles. (Plates VII, XVIII, and XIX.)

A few separate feeding-scars of the adult beetles do no appreciable damage, but when the scars are crowded together the whole of the attacked part of the leaflet dies. Leaflets severely attacked in this way eventually die back basally rather further than the limit of the feeding-scars, so that even when only a third of a leaflet is attacked at least half of it dies in consequence. In the later stages of severe outbreaks, the whole of the distal half, at least, of every leaflet, without exception, is killed, and the uniform distribution of the damage throughout each tree is remarkable, except that whereas in the proximal half of each leaf, the leaflets do not usually die back further than their middle points, in the distal half of each leaf they often die back further, so that only their proximal thirds remain unaffected by the adult feeding-scars. This is due to the preference shown by the adults, particularly during the pre-copulation period when they are markedly gregarious, for the more distal leaflets. In the intermediate stages of an outbreak the leaflets in the distal half of each leaf are dead and withered at their extremities, while those in the proximal half are still normally green and straight, and not appreciably damaged. This is the condition which is most frequently seen, and it is very characteristic.

In the early stages of an outbreak, only the 3 or 4 youngest leaves are severely attacked by the adults, these being the ones that they prefer during their gregarious period. During their oviposition period, they feed on the older leaves also, but less gregariously and not only at the tips of

the leaflets, and therefore the older leaves are not appreciably damaged at first, the feeding-scars on them being, for the most part, well separated. As generation succeeds generation, however, the damage accumulates, and the leaves which were young when the outbreak began are replaced by others and become old, so that although gregarious feeding is always largely confined to the youngest leaves, in the later stages of an outbreak all the leaves are damaged to an equal extent.

The damage done by the adults is always more noticeable at a distance than that done by the larvae, since the adults attack those parts of each leaf which are the most conspicuous—namely, the distal parts of the distal leaflets.

3. **Damage Done by Larvae.** (Plates VI, VII, VIII, IX, and XIX.)

A single mine, which is not close to other mines, causes the death of exactly that area of leaflet which it occupies, and no more; but in the last stages of severe outbreaks there is, in the older leaves, a great accumulation of mines representing many generations, and these are so close together that the unattacked tissue between them dies long before it otherwise would, although long after most of the mines concerned were made.

The eggs are not usually laid at the extreme bases of the leaflets, and therefore almost all the leaflets remain entirely undamaged by mines near their bases. Moreover, since the eggs are orientated so that their anterior ends are directed towards the tips of the leaflets, almost all the mines have their narrower ends nearer the bases of the latter, and therefore even in very severe outbreaks nearly all the leaflets are always green over a distance of about 4 inches from their proximal extremities (Plate VIII, b). Except in this proximal portion, however, the tissues of every leaflet are eventually almost wholly killed, the mines occupying nearly all of that part which lies between the end of the green basal portion and the proximal end of the distal portion killed by the adult beetles. The oldest leaves, in which mines and adult damage of several generations have accumulated, are almost wholly dead, and they tear and break in the wind so that they present an extremely ragged appearance.

The 3 youngest leaves normally contain new mines only, representing only one generation, because in the period covered by one generation of the pest 3 new leaves develop. But each leaf, as it becomes older, is increasingly damaged, and by the time that it becomes the 4th on the tree (if we call the youngest the 1st), it begins to accumulate mines which represent a second generation, and then, even at this comparatively early age, it is defoliated to the extent of at least 40% if the outbreak is already far advanced. Leaf 1 usually contains no mines, partly because it usually has not been fully open long enough for the eggs laid on it to have hatched, but chiefly because the beetles, when ovipositing, avoid the youngest leaf of all. Leaf 2, except on certain occasions in one-stage outbreaks to be described later, contains many mines. Leaf 3 is very severely damaged, and although the number of mines on it is less than on the older leaves, this leaf, in the later stages of outbreaks, usually contains more larvae, actually living at the time, than any other leaf on the tree; and the reason for this is that the beetles, although not normally preferring the younger leaves for oviposition, are obliged in these circumstances to lay

more eggs on them than on the older ones because the latter have very *little green tissue left.*

### 4. The Condition of Maximum Defoliation.*

Until an outbreak has been in progress for several generations, the beetles exhibit a marked reluctance to spread. So long as the trees are more green than brown, no appreciable spreading takes place, and the consequent concentration of all of them within the same area, generation after generation, causes the trees to be defoliated at the maximum rate possible. There comes a time, however, when the defoliation is so great that the beetles are induced to spread to new areas in enormous numbers, and from this time onwards the defoliation does not increase, because the tendency to spread persists and is controlled by the degree of defoliation. The spreading always occurs before the trees are completely defoliated, being due, not to food shortage, but to lack of sufficient space for the beetles' requirements when ovipositing. Consequently, maximum defoliation is never total defoliation, but is the degree of defoliation reached at the time when spreading commences. The time which elapses from the *absolute commencement of an outbreak until maximum defoliation is* first reached is normally 4 generations or 14 months, the mean duration of one generation being 3·5 months. When the beetles have spread to new areas, however, maximum defoliation is reached in these areas in *only 2 generations, because the initial population in the new areas is* infinitely greater than the population from which the outbreak developed in the original area.

In one-stage outbreaks it is impossible for maximum defoliation to be maintained constantly, since the beetles are absent for about 2 months in every 3½ months. In these 2 months, 2 new leaves are produced and there is nothing to attack them, and the leaf which was the youngest when the last generation of adults was present was then only slightly attacked. Consequently, by the time that the next generation of adults begins to appear, the tree is bearing 3 functioning leaves, almost entirely undamaged, and the total defoliation is less than the maximum. The new adults, however, now attack these healthy leaves very severely and maximum defoliation again obtains. In one-stage outbreaks, therefore, *maximum defoliation recurs every 3½ months, and the trees suffer slightly* less than in multiple-stage outbreaks, in which it is maintained continuously. The periodic presence of the 3 green leaves in one-stage outbreaks causes each tree to look noticeably greener, with the result that observers often report optimistically that outbreaks are diminishing when actually, as they discover a month later, the pest is as abundant as ever.

A numerical estimate of maximum defoliation was obtained by selecting a typical tree and cutting from each of its 30 leaves 4 leaflets—2 from the middle of the proximal half of the leaf and 2 from the middle of the distal half. The average defoliation for the 4 leaflets was then determined approximately by direct measurement, and this represented, with sufficient accuracy, the defoliation for the whole leaf. The results were :—

* The term "defoliation" is here used to mean reduction in the functioning leaf surface, not the actual removal of the leaves from the trees.

On leaves 1, 2, and 3, defoliation = 12% (mean)
,, ,, 4, 5, and 6, ,, = 40% (each)
,, ,, 7, 8, and 9, ,, = 70% ( ,, )
,, ,, 10–14 ,, = 80% ( ,, )
,, ,, 15–30 ,, = 90% ( ,, )

By summing the percentages for all of the 30 leaves an estimate for the tree as a whole is obtained. This works out at 73·5%, and this is the maximum defoliation. It is not possible for the defoliation to exceed this percentage, except slightly in special cases, because the limit is set by the habits of the beetles themselves and by their rate of multiplication in conjunction with the rate of production of new leaves.

The extent of the defoliation due to the larvae is approximately equal to that due to the adults when maximum defoliation has been reached. On the youngest leaves the defoliation by the adults is greater than that by the larvae, and on the oldest leaves the reverse is the case. Measurements of the adult and the total damage on typical leaflets of every third leaf of a typical tree gave an estimate of approximately 50% for the adult damage on the tree as a whole.

In order to estimate the population of adult beetles which corresponds to the condition of maximum defoliation, a typical tall tree in a one-stage outbreak was selected in 1933 in area K at Nabavatu (Map II) at a time when the egg stage was the dominant one (*i.e.* when all the adult beetles had emerged), and certain leaves were cut and the numbers of mines of the most recent generation which contained adult emergence holes were counted. (The mines of the most recent generation are readily distinguishable from all older ones by their appearance and texture.) The leaves selected were Nos. 1, 2, 3, 6, 9, 16, 20, and 23. Leaves 1 and 2 had yielded no beetles, having been produced since the eggs were laid. Leaves 3, 6, 9, 16, 20, and 23 produced 93, 372, 250, 156, 66, and 0, respectively. All the leaves after and including No. 23 produced no beetles because there was no room for mature mines on them. A general inspection of leaves 5 and 7 *in situ* showed that they contained rather fewer mature mines of that generation than No. 6, which therefore contained the maximum. By allotting equal increments to the leaves whose mines were not counted, the following figures were obtained :—

| Leaf. | No. of Mines. | Leaf. | No. of Mines. |
|---|---|---|---|
| 1 | 0 | 13 | 195 |
| 2 | 0 | 14 | 182 |
| 3 | 93 | 15 | 169 |
| 4 | 186 | 16 | 156 |
| 5 | 279 | 17 | 133 |
| 6 | 372 | 18 | 110 |
| 7 | 332 | 19 | 88 |
| 8 | 291 | 20 | 66 |
| 9 | 250 | 21 | 44 |
| 10 | 236 | 22 | 22 |
| 11 | 222 | 23 | 0 |
| 12 | 208 | 24 (*et seq.*) | 0 |

Adding up all these figures, the total for the tree is 3,634 beetles for the one generation, and this, approximately, is the maximum population per tree which the habits and biotic potential of the species, and the rate of production of leaves by the tree, permits. For practical purposes, the beetle population per tree may be estimated at 4,000, or 4 million per thousand trees, and this is of great importance in connection with biological control. The same figure, approximately, was obtained in other localities by less extensive counts.

*It is important to bear in mind that the number of eggs or larvae of any one generation, after the maximum population has been reached, is in excess of the number of adults resulting from them because by this time the natural enemies have become numerous and are destroying both eggs and larvae.*

The above figures apply equally, but with slight modification, to multiple-stage outbreaks. In these outbreaks, the number of beetles produced in one tree during the period covered by one generation ($3\frac{1}{2}$ months) is 4,000, but the adult population at any one time is only about 1,300 because the adult life covers only about a third of the period of one generation.

In any typical outbreak, the total number of egg-capsules and mines, of all generations, present in one tree two generations after maximum defoliation is reached (*i.e.* 6 generations from the absolute commencement of the outbreak) is usually about 60,000, but frequently reaches 80,000. This is the total number of individuals which have, at one stage or another, been present in that tree since the outbreak began,* and this number is not appreciably exceeded later because by this time the outbreak (within that particular area, but not in the neighbouring areas more recently infected) is rapidly being suppressed by natural enemies. The total number of adult beetles which the tree has produced since the outbreak began is, however, very much less than 60,000, and is, in fact, about 15,000 (*i.e.* about 25% of the number of eggs laid in it), judging from counts on typical leaves, and allowing for the leaves which have fallen from the tree. This is equivalent to 4,000 (the maximum population) for 3 generations, together with the beetles which emerged previously. *Thus, neither the maximum population of beetles at one time, nor even the total number of beetles produced, approaches the number of eggs laid.* On a leaflet of average size,† there is room for 12 mature mines, allowing for adult damage, but actually there are never as many as 12 because the eggs are never arranged in the ideal manner. In order to ascertain how many larvae a leaflet of average size, damaged to the average extent by the adult beetles, can in reality support, 20 unmined leaflets, fulfilling these conditions and also bearing 12 or more eggs, were selected in the field, no attention being paid to the arrangement of the eggs, and were screened from parasites by cloth bags. It was found that, in the absence of natural enemies, but in otherwise normal conditions,

* Many of the egg-capsules of the first few generations have dropped from the tree by this time, but the numbers present in the first few generations are negligible by comparison with the total after 6 generations.

† The size of the leaflet varies greatly according to its position on the leaf. The smallest leaflets can contain only 2 mature mines.

the typical leaflet can support 8 larvae, on the average, to maturity, but not more although it contains enough tissue to feed more had the eggs been arranged differently. Therefore, since the number of leaflets per leaf is about 200 and the number of leaves per tree about 30, the maximum beetle-producing capacity of one tree in the absence of natural enemies is 48,000, or approximately 3 times the number which it actually produces, and considerably less than the total number of eggs laid in it. The discrepancy between the beetle-producing capacity and the number of beetles actually produced is due to two factors: first, the egg and larval parasites, which increase in successive generations and cause heavy premature mortality in the later generations; and secondly, excessive oviposition, and consequently overcrowding of mines, particularly on the leaflets of the proximal halves of the leaves. These two factors cause the total number of beetles produced per tree never to exceed about 30% of the beetle-producing capacity of a tree.

5. **Appearance of Attacked Trees.** (Plates XVIII and XIX.)

When a tree is first attacked, the damage done is not conspicuous, and unless a special search is made, the presence of the pest often remains unsuspected for many months. During the early stages of an attack, the tree or trees concerned look, at a glance, as green and healthy as those which have not been attacked at all, but a close inspection by means of field-glasses reveals the fact that the tips of some of the leaflets in the distal thirds of the youngest leaves are withered, dead, and brown, while on a few of the leaflets elongate brown scars, which are the mines, can be detected, and these, unlike the withered tips, are more numerous on the older leaves.

The damage done first becomes conspicuous about 6 months after the commencement of an attack. By this time, the tips of the leaflets of many of the older leaves, as well as those of all the youngest leaves, are dead, and mines are numerous and are visible without the aid of field-glasses. The general colour is still green, however.

After 3 more months, the tree or trees concerned are obviously severely damaged, and, at a glance, are conspicuously different in appearance from their unattacked neighbours. They have assumed a brownish-grey colour as if they had been badly burned, and have acquired a very dishevelled appearance which is due to the fact that the extremities of all the leaflets of all the leaves are now dead and curled over.

Eventually, when the outbreak has covered a wide area, the ravages of the pest can be recognised and are noticeable from a long distance. If the attacked area is a coastal belt, as it very frequently is, the damaged trees, when viewed from a mile or more out to sea, form a light greyish line along the coast, very different from the usual bright-green line which is so familiar to everyone who is accustomed to tropical islands. This stage is not reached until about 2 years after the commencement of the attack and at least one year after the tree or trees first attacked became more brown than green.

At all stages of an outbreak, however, the 2 or 3 youngest leaves of every tree are mainly green.

### 6. Ultimate Effect upon the Trees and the Crop.

The severe defoliation causes the trees to produce leaves which are smaller and weaker than usual, but the rate at which new leaves are produced is not appreciably reduced. Another result of the defoliation is that the rate of production of flower-spikes, and therefore of fruits, is very greatly reduced, and in extreme cases the trees cease flowering altogether for several months. There is also a great increase in premature nutfall. The number of female flowers (*i.e.* potential nuts) which a coconut tree produces per flower-spike is always considerably in excess of the number of nuts which it can support to maturity, and therefore considerable premature nutfall always takes place and is perfectly natural, even on healthy trees. This natural nutfall, however, takes place, for the most part, when the nuts are very small. The ravages of *P. reichei* cause the nutfall to continue very much longer, relative to the age of the nuts. Many nuts, which would ordinarily develop to maturity, drop from the trees when they are half-grown. This, together with the decrease in the rate of production of flower-spikes, results in a very considerable reduction in the crop for the area affected.

The reduction in the crop is most noticeable in the year following that in which maximum defoliation has been reached and the outbreak has terminated. The maximum extent of the reduction for the year is 60%, and this is by no means unusual in the Lau Islands. The average reduction for all areas in which maximum defoliation has been reached is in the neighbourhood of 50%.

## B. The Nature, Distribution, Causes, and Limitations of Outbreaks.

### 1. Islands on which Outbreaks Occur.

It has already been pointed out that *P. reichei* appears to be present throughout Fiji on all islands where coconuts are plentiful. Since it is well-known as a serious pest on some islands, it would be reasonable to assume that it is liable to be an equally serious pest on all. Yet observations made over a long period of years show that although it is present on all islands it is seldom a pest of major importance except in the Lau (or eastern) Group.

This is, in fact, one of the most striking and peculiar features of the outbreaks. They occur from time to time on many islands which are not in Lau (notably Vanua Levu, Taveuni, Rabi, Koro, Ovalau, and Kadavu), but although in all these cases the resulting defoliation on the trees concerned is sufficient to justify the term " outbreak," the number of trees involved and the total area covered in each case are as a rule so small that the damage done is almost negligible. Nearly all the outbreaks on these islands are controlled by natural means long before they attain dangerous proportions, and outbreaks of this kind have occurred for so long without showing any tendency to become more serious, that *P. reichei* can definitely be said to be of little economic importance in all parts of Fiji except Lau. A typical instance of such an outbreak is one which occurred at Matana Plantation, Koro, in 1927. The total area affected

measured about 250 yds. × 25 yds. Within this area all the trees were attacked and many were considerably damaged, but the neighbouring trees were scarcely attacked at all and the outbreak cleared up without spreading any further. Very frequently the affected area is even smaller than this, and occasionally only a single tree is affected, the pest being abundant in this one tree but not spreading appreciably to neighbouring trees before the outbreak is terminated by natural agencies.

In Lau, on the other hand, this insect is a pest of very considerable importance. Outbreaks attain large dimensions, covering hundreds of acres and seriously damaging many thousands of trees. The island of Kanacea is a particularly striking example. Almost the whole island, which measures about 10 miles round the coast, is planted with coconuts, even to the tops of the hills. Almost all the trees are tall, and, in ordinary circumstances, very flourishing. In 1929 the whole island, apparently without the exception of a single tree, was covered by the pest.

It is important to notice that although, on the whole, this difference between Lau and the rest of Fiji is very marked, outbreaks of dimensions comparable to those in Lau occur, though very rarely, in other parts of Fiji. The difference must therefore be regarded as a matter of degree only, and cannot be said to be absolutely constant.

The islands in Lau which are mainly concerned are Vanua Balavu, Kanacea, Mago, Cicia, Munia, Naiau, Lakeba, and Yacata.* These islands form a natural group, which may be termed Northern Lau and must be regarded as the stronghold of *P. reichei*. There is, however, one island in Northern Lau, Naitauba, which has in the past been anomalous as regards *P. reichei* in that no extensive outbreak has ever occurred there, although small, negligible, outbreaks, comparable in extent to those which are characteristic of other parts of Fiji, are of frequent occurrence.

In the rest of Fiji, small outbreaks occur on almost all the islands occasionally, but the island Rabi is the only one on which outbreaks of serious dimensions occur frequently.

In general, therefore, *P. reichei* is a pest of primary importance in the Lau Group only. The two exceptions to this rule, Naitauba and Rabi, are discussed in a later section.

### 2. The Climatic Conditions in which Outbreaks Develop.

The climate of the Lau Group, where outbreaks are most severe and most frequent, differs from that of most other parts of Fiji. There is no great difference in temperature, humidity, or wind, but there is, in general, a great difference in rainfall. An imaginary line running north and south between the Lau Group and Taveuni divides Fiji into two groups of islands of which one, the western group, considered as a whole, has a much greater rainfall in both the wet and the dry seasons than the other, the eastern group. Topographical differences account for the difference in rainfall, for whereas the western group contains several large and lofty islands, of which the three largest rise to a height of more than 3,000 ft. while all the others except the smallest are about 2,000 ft. high, the eastern group contains islands all of which are relatively small and are less than

* For administration purposes this island is not included in the Lau group, but geographically and climatically it belongs to that group.

1,000 ft. high, the majority of the largest being between 500 and 800 ft. high. The same imaginary line serves almost equally well to divide Fiji into two regions characterised by the extent and frequency of outbreaks of *P. reichei* in them : in the western group, outbreaks are of rare occurrence and are very seldom extensive; in the eastern group they are of very common occurrence and are nearly always very extensive. The natural enemies of *P. reichei* are the same on both sides of the line, and *P. reichei* itself is present on all the larger islands throughout Fiji. Of the differences, other than rainfall, which exist, such as differences in topography, flora, and fauna, there is none which concerns *P. reichei.* It is therefore evident that the much smaller rainfall in Lau accounts for the frequency and severity of the outbreaks there, and it would seem reasonable to suppose further that a heavy rainfall is a direct cause of the death of the insect, in one stage or another.

Observations and experiments have shown, however, that only rain storms of exceptional severity and unusually long duration are detrimental to *P. reichei.* Ordinarily heavy rains, such as those which occur in all parts of Fiji during a normal wet season, are in no way detrimental to it in any stage, and it continues to thrive throughout every normal wet season unless suppressed by natural enemies. Moreover, the closely allied *P. nuciferae* in Java, whose habits are very similar to those of *P. reichei* and whose larvae mine in coconut leaves in exactly the same way as *P. reichei*, thrives in certain localities which have a rainfall greater than that of most parts of Fiji. Hence, although there is no doubt that rainfall largely determines the extent and frequency of outbreaks, its action upon the pest is indirect.

A detailed study of the natural enemies of the pest has shown that the reason for the greater severity and frequency of Lau outbreaks is in reality due to the fact that the Lau rainfall is not sufficient to suppress the mite, *Pediculoides ventricosus*, which is the normal cause of extensive outbreaks and upon which rainfall has a very detrimental effect.

The larger western group of islands, although as a whole much wetter than Lau, includes certain islands, notably the Lomaiviti islands and Kadavu, and certain parts of islands, notably the north coast of Vanua Levu, whose rainfall is approximately the same as that of Lau. These islands and parts of islands are represented in Table I (see p. 18) by the localities numbered 4, 7, 14, 15, and 16, while the Lau localities are numbered 1, 2, and 3. In these drier parts of the western group, outbreaks of *P. reichei* occur with comparative frequency and are almost all of the one-stage type, due to the mite. They are, however, much less extensive as a rule than the Lau outbreaks, and for this there are two reasons. Firstly, in most of these localities there are no large coconut estates extending far inland, the palms being confined either to narrow coastal belts or to small, widely separated, groups. In these circumstances the pest is greatly restricted in its spreading, and the Hymenopterous enemies, which are the normal controlling factors, are not prevented from overtaking it numerically. In Lau, on the other hand, the palms are mostly on estates which cover large areas and extend for long distances inland as well as along the coasts, and the pest repeatedly spreads ahead of its natural enemies sufficiently to prevent them from overtaking it numerically

before it can spread further. This factor clearly has no connection with climate and operates, regardless of rainfall, in all parts of Fiji. The second reason for the less extensive nature of these outbreaks is that in many of the localities concerned the rainfall in the drier season, although not very different in amount from that of Lau, is distributed fairly evenly in normal years, so that the periods of drought are not nearly so extreme as in Lau. The result is that the mite is less thorough and does not eliminate completely all stages except one, either initially or subsequently, although it causes one stage to predominate. Partial overlapping of generations consequently occurs and the Hymenopterous parasites are not handicapped nearly so severely as in Lau. These outbreaks are, in fact, intermediate in this respect between the multiple-stage and one-stage types (as is very evident when the mines are opened and their contents examined), and their extent is consequently intermediate also.

Outbreaks occur also in very wet localities in Fiji, such as Taveuni and the wet southern coast of Vanua Levu. These are usually very restricted and comparatively harmless. Their restricted nature is not due to any direct effect of rainfall upon the pest but to its effect in maintaining the mite in a condition of extreme rarity. These outbreaks are of the typical multiple-stage form and are inherent in the normal wave-like equilibrium between the pest and its Hymenopterous parasites. They are liable, in periods of abnormally little rain for the localities in question, to be partially transformed by the mite into the one-stage type, and on such occasions they become more severe until the mite is again suppressed by rain, but for the most part they are economically negligible, being checked by the Hymenopterous parasites before they attain serious dimensions.

With regard to the actual amount of rainfall necessary to prevent the mite from causing the one-stage condition, a study of rainfall statistics and of *P. reichei* records shows that extensive outbreaks rarely occur in localities where the annual rainfall always exceeds 100 ins., and that they are of common occurrence in many localities whose annual rainfall is less than 80 ins. (*e.g.* the Lau Group). These two amonnts, 80 ins. and 100 ins., may be regarded as the critical amounts, but as such they are only applicable if the rainfall is distributed so that there are no long periods of extreme drought. Localities whose rainfall lies between 80 and 100 ins. are liable to outbreaks intermediate in severity, again assuming that the rainfall is well distributed. In the Lau Group, periods of extreme drought covering 2 or more months are of almost annual occurrence and it is these which, by favouring the mite, are largely responsible for the extent of the Lau outbreaks. In a few other parts of Fiji, periods of drought, comparable to those of Lau, occur almost annually, and outbreaks result, but in these parts the outbreaks are limited because the coconuts themselves are limited and the pest cannot easily spread. The distribution of rainfall during the year, therefore, is of even more importance than the total annual amount, and for this reason the figures given above must be regarded as indications only, not as definite limits.

### 3. The Situations in which Outbreaks most frequently arise.

Not only do outbreaks occur more frequently and attain larger dimensions on certain islands than on others, according to climatic conditions, but also they arise more frequently in certain parts of islands than in other parts. The islands most subject to severe outbreaks are, as we have seen, the dry, isolated ones. The parts of islands which are mostly affected cannot be defined quite so easily. Outbreaks are liable to arise in any locality whatsoever, whether coastal or inland, elevated or at sea-level, exposed or sheltered: but there are, nevertheless, certain rules which apply to the majority of cases in both the wet and the dry zones.

In all parts of Fiji outbreaks most frequently begin on coastal flats, or, in the case of islands which have no coastal flats, on trees growing by the sea at the bases of the hills. Moreover, the great majority of outbreaks begin on those trees which are nearest to the sea and are growing almost on the beaches. In the wet zone, the outbreaks not only begin near the sea but also seldom extend far from it, being restricted, as a rule, to small groups of trees near the beach. On the islands in the dry zone they nearly always begin by the sea but usually extend inland subsequently.

A noticeable feature of most outbreaks is that they begin on trees which are exposed to the prevailing wind (*i.e.* wind from the S.E.). This rule, however, is very elastic. In Lau, outbreaks commonly begin in completely sheltered places, although the majority begin in exposed ones.

The most noticeable fact, however, in connection with the places in which outbreaks begin, is that the great majority begin near landing-places, native villages, and European homesteads. Since nearly all native villages are coastal and most European homesteads are built near the best landing-places, it is true to say that most outbreaks begin near landing-places; but it is nevertheless noteworthy that on the few islands where there are dwellings far inland, the few outbreaks which begin inland usually do so in the neighbourhood of the dwellings.

Thus, while it is important to remember that there are many exceptions, it can be said, as a general rule, that the majority of outbreaks begin in exposed places near the sea, most frequently near landing-places. There are two main reasons for this. Firstly, a frequent cause of outbreaks is the accidental introduction of a few pest individuals in the coconut leaves used by the natives for making baskets, and the baskets are usually taken to native villages or European houses and are seldom deposited inland. Secondly, the two natural enemies which are the principal controlling factors are hampered by strong winds, so that their controlling influence is less intense in exposed places.

### 4. The Causes, Course, and Termination of Multiple-Stage Outbreaks.

a. *Causes and Commencement.* We have seen that the oviposition period of *P. reichei* covers about 2 weeks, that the extent of the variation in the duration of the life cycle is 1 week, and that the mean period of one generation is $3\frac{1}{2}$ months. From this it follows that if a single paired female is released in a locality in which the species has not previously been present, complete overlapping of generations must result after about

$3\frac{1}{2}$ generations, the variation in age of the immediate progeny of any one beetle during this time being (on the average) 21 days while the oviposition period of the immediate progeny covers 35 days. Thus, the multiple-stage condition is established comparatively soon. In fact, it is inevitable, and must persist indefinitely, unless some factor of an unusual nature intervenes.

*The normal mode of occurrence of the pest is such that it is very local*, mainly on account of its gregarious habits, and remains within the same small areas for long periods, often for years. In these small areas, however, its population is not constant, but wave-like. The insect is controlled by its indigenous enemies, but the equilibrium is unstable. The pest and parasite populations increase periodically, the latter at the expense of the former. *The maximum pest population reached at the* end of each period of increase is sometimes great enough to cause damage to the trees and sometimes is not. In the former case, the term "outbreak" is applicable, and in the latter it is not, but the difference is only a matter of degree. *During every period of increase of the pest, the multiple-stage condition is inevitably established and maintained.*

Multiple-stage outbreaks, therefore, are within the normal scope of the equilibrium between the pest and its parasites, and the instability of the equilibrium is the most normal and the most frequent cause of them. That is to say, outbreaks of this type occur in localities where all the indigenous parasites are present and normally active. In exposed situations, where the activities of the parasites are hampered by strong winds, these outbreaks attain a greater degree of severity.

Multiple-stage outbreaks also occur, however, in localities where the indigenous parasites are absent. The presence of the pest without its parasites may be brought about either by the removal of pest individuals to new areas or by the elimination of the parasites in areas in which they have previously been present.

The removal of pest individuals from one area to another which is not adjacent, and from one island to another, occurs very frequently and is almost invariably due to human agency. That it can result comparatively soon in the multiple-stage condition, even if only a few adults are introduced initially, we have already seen. The leaves of the coconut palm are very extensively used by the natives throughout the islands for making baskets in which they carry produce of all kinds from village to village and island to island. Whenever the leaves are cut in areas in which outbreaks are raging, all of them invariably contain mines, and after the leaves have been made into baskets the mines are carried to other places. If the mines happen to contain prepupae, pupae, or newly-emerged adults when the leaves are cut, the pest individuals do not suffer as a result of the death of the leaves and can survive journeys of long duration and complete their development. Individuals which are prepupae when the leaves are cut can survive a journey lasting about a month (in the cool season) and emerge as healthy adults at the end of it. The writer has seen mines in abundance in baskets on ships and in baskets carried by natives, and in these baskets the pest is carried from one part of an estate to another, from one part of an island to another, and from island to island, near or remote. Frequently all the individuals are

crushed when the basket is made or during the journey, but occasionally some survive, and these cause outbreaks if they happen to emerge from the mines in places where the pest was not previously present.

Occasionally the adult beetles fly on to ships which are anchored near the shore, but probably this only occurs after exceptionally heavy rains when the beetles fly in large numbers near the ground and for short distances out to sea. Beetles which fly on to a ship just before sunset remain on it all night, and if the ship travels overnight they may be carried to another island. That this occasionally happens there is no doubt, but it is certainly a rare event.

The occurrence of the pest without its natural enemies is most often caused, therefore, by human agency, pest individuals being introduced into new localities. The other means by which the absence of natural enemies can be caused is the elimination of the natural enemies themselves, and this is brought about by hurricanes, and by no other factor.* That hurricanes are very detrimental to the pest as well as to the parasites is obvious, but the parasites on account of their much smaller size and greater frailty, suffer much more than the pest. The mines are ripped open and their contents fall out, or are washed out by the rain. The egg-capsules of the pest, healthy and parasitised alike, become soaked with water and are displaced from the leaves. The leaves are broken and subsequently die, and the pest and parasite individuals which remain in the mines die through lack of food. The adults of the pest and of the parasites are carried away by the wind, and no doubt a very large proportion of them die. Many are carried out to sea, while others are carried inland, when the wind changes, to places where there are no coconuts. These and many other results of hurricanes cause the death of both the pest and the parasites in all stages, but whereas the latter are completely eliminated, the former survives in sufficient numbers to commence breeding again at once. It is most probable that the pest survives in the adult stage in larger numbers than in any other stage, because the adults drop to the ground before the full force of the storm is upon them. However this may be, the very few parasites which survive, if indeed there are any, have the greatest difficulty in finding eggs or mines of the pest in which to oviposit. The pest can therefore start afresh and there is nothing to check it. For many generations it maintains its initial advantage, and multiple-stage outbreaks of quite abnormal dimensions result in localities where the pest and its parasites were formerly in equilibrium and where there would otherwise have been either no outbreak at all or merely restricted and almost negligible ones controlled almost as soon as they developed by the natural enemies. Fortunately, hurricanes are comparatively rare events, and multiple-stage outbreaks of this nature are correspondingly rare. In 1931 and 1932, however, several severe outbreaks arose as a result of the hurricanes of the 1930–31 season, and for very many years planters have commented upon the prevalence of the pest after hurricanes.

The time of commencement of the outbreaks in which the parasites are initially present and in unstable equilibrium with the pest is simply

* There are no secondary parasites or other enemies which can completely or almost completely eliminate both of the primary parasites.

the time at which the pest population begins to increase after a period of decrease. At such a time the insect is extremely rare, and on account of its rarity the commencement of the increase cannot be observed and the time at which it occurs, relative to the times of maximum population, is always unknown. There is no reason to assume that it is midway between successive times of maximum population. However this may be, the outbreak begins with all stages of the insect present simultaneously but in a condition of great rarity, and the same applies to the parasites except that their rarity is even greater. The parasites are greatly handicapped at this time, in their search for host individuals suitable for the reception of their eggs, by the great rarity of the pest, and consequently, the percentage parasitism is very low. The multiplication of the pest therefore proceeds at first at almost the maximum rate, and is continuous because all stages are present.

In the case of those outbreaks which result from the initial absence of natural enemies, the conditions at the commencement are quite different. Only adults of the pest are present initially, and these are very few. These adults lay their eggs and die, and there is no further multiplication until the individuals which result from the eggs become adult. The difference in age between the oldest and youngest individuals in this first generation can never be more than a month, and in the case of outbreaks which result from a few individuals introduced as pupae in their mines from another area, the difference of age in the first generation may not be more than 2 weeks (*i.e.* the duration of the oviposition period). At first, therefore, one stage is markedly dominant at any one time, but the conditions are not those which lead to a one-stage outbreak.

b. *Increase and Spread of the Pest.* All multiple-stage outbreaks develop rapidly for the first two generations at least, because initially the parasites are absent or, if present, are ineffective. If the parasites are present initially, however, they can, after a period equal to 2 pest generations, multiply at their maximum rates, because by this time the pest is abundant and because it has not spread. It usually happens, therefore, that the parasites suppress the pest after about 9 months, when the trees concerned are rather severely defoliated but maximum defoliation has not been reached. The pest remains all the time in the same trees because the tendency to spread does not arise before maximum defoliation is reached, and therefore the outbreak is confined to a small group of trees and sometimes to a single tree.

When the parasites are absent initially, the outbreak proceeds much further. The extent to which successive generations overlap increases with each generation until, in its 4th generation, overlapping is complete, all stages being present simultaneously. Maximum defoliation is usually reached by the end of the 4th generation, and the pest then begins to spread, the spreading being gradual. From this time onwards, spreading from the original area is continuous, and the rate of spread and the rate of production of new leaves are such that the pest population within the original area remains constant. The beetles spread in all directions, unless they are prevented from spreading uniformly by topographical barriers, and the width of the newly-infected area is about 200 yards, regardless of the number of trees in the original area and

therefore of the number of beetles which spread from it in a given time. The pest now remains within the boundary of the new area, since there is no further inducement to spread. It multiplies within the new area and its population therein is constantly supplemented by beetles which spread from the old area. The number of generations spent in the new area before further spreading takes place depends upon the number of trees in the original area; for if the outbreak initially covered only a few trees, or, as is often the case, a single tree, the population per tree in the new area is initially very low, whereas if the original area included 20 trees or more, the initial population is much larger, the new area being approximately the same extent in each case. In some outbreaks, maximum defoliation and population in the new area are not reached until the 4th generation after spreading commenced, but in other cases they are reached after 2 generations. Further spreading now takes place, again through the same distance, and in this second new area the initial population is sufficiently high to cause maximum defoliation and population to be reached in 2 generations. Thus, from this time onwards, new *areas are infected every second generation* (*i.e.* *every 7 months*), *and the total area over which maximum defoliation has been reached, and from which spreading is continuous, increases every 7 months by the addition of one new area. It is important to notice that although all stages, including beetles, are present simultaneously, and spreading within the infected area is continuous, spreading to new areas is periodic only.*

Multiple-stage outbreaks which result from hurricanes may continue for 2 years and become very extensive. This is due to the elimination of the parasites over very wide areas. On the other hand, multiple-stage outbreaks which result from the introduction of a few beetles into a new area rarely attain very large dimensions because they are usually discovered comparatively soon by the parasites, which, if not initially present in the immediate vicinity, are usually present in some locality nearby. In these outbreaks, therefore, spreading to one new area usually takes place, but to one only.

c. *Termination.* The termination of multiple-stage outbreaks is normally brought about by the indigenous Hymenopterous parasites (*Elasmus hispidarum* and *Oligosita utilis*). The time comes when the larval parasitism by *Elasmus* reaches or approaches 100%, and this happens before the egg parasite has attained 100% parasitism. Both parasites can breed continuously, but the life cycle of *Elasmus* is very much shorter than that of *Oligosita*, and consequently the former multiplies more rapidly. The complete elimination of larvae by *Elasmus* appears to continue for about a month, and includes those larvae which emerge from eggs during that time. This causes very great reduction later in the population of adult beetles, and this reduction is enhanced all the time by the egg parasite. After this, however, the suppression of the pest is much more gradual, and eventually it ceases before the pest is entirely wiped out. The parasites first become numerous in the area in which maximum defoliation has been reached, and then, after the pest population in that area has been reduced to the new low level, they reach their maximum abundance in the surrounding, less defoliated area, and reduce the population there also to a low level. There is then an

excess of parasites in the surrounding area, and extensive invasion of the more central area consequently takes place, and the pest population in the latter area is now reduced almost to nil. This process is repeated in both directions, alternately, and it finally results, in most outbreaks, in the complete elimination of the pest throughout the outbreak area except in a few places in the area most recently infected by the pest. In these few, widely separated, places, or sometimes in one place only, a few pest individuals remain, and in these localities the multiplication of the pest begins once more in the presence of the parasites, the normal unstable equilibrium having been established.

In the small outbreaks in which the parasites are present from the beginning and the pest is suppressed before it spreads, the elimination of the pest is never complete, unless abnormal factors supplement the effects of the parasites. The pest is gradually reduced to a condition of rarity and the parasites necessarily become even rarer, and then the pest begins to multiply again. On this occasion it may or may not be permitted to become sufficiently numerous to constitute an outbreak before it is again suppressed. In these circumstances, the pest remains within the same small group of trees for years, showing no tendency to spread but increasing periodically and at long intervals of many months, and usually rather more than a year (*i.e.* the period covered by 4 or 5 generations).

Outbreaks are occasionally terminated by abnormally heavy or protracted rain, which causes the death by drowning of all stages except eggs and adults. One spell of heavy rain cannot terminate a multiple-stage outbreak, but if it is followed after 3 or 4 weeks by another, also of abnormal severity and duration, the young larvae which have resulted from the adults and eggs which survived the first spell are destroyed and nothing remains.

### 5. The Cause, Course, and Termination of One-Stage Outbreaks.

a. Pediculoides ventricosus *as the Cause of the One-Stage Condition and of its Continuance.* All one-stage outbreaks, without exception, arise from pre-existing multiple-stage outbreaks, and the causes of the latter are therefore the initial causes of the former. The transformation from the multiple-stage to the one-stage condition is invariably effected solely by the mite, *Pediculoides ventricosus*. The mite, however, not only causes the one-stage condition, but also maintains it indefinitely, and its ability to maintain it is the principal reason for the severity of one-stage outbreaks. The persistent lack of overlapping of generations in these outbreaks is particularly remarkable when it is considered that complete overlapping ordinarily and inevitably occurs, as we have already noted, after only 3 generations, even when only one beetle is present initially.

The activities of *P. ventricosus* in outbreaks of *P. reichei* are complex and peculiar. In almost any area in which a severe one-stage outbreak is raging, the mite succeeds, at the end of the dry season, in attaining almost 100% parasitism in the pupae then present, and an observer who chanced to inspect such an area at this time would say at once that the outbreak was finished and that the pest had been almost completely wiped out by the mite. But he would, in most cases, be wrong, in spite

of the 100% parasitism which he observed. If he were to return 6 months later, he would probably find the outbreak still raging in the original area, and severe outbreaks developing in all neighbouring areas. It is reasonable and usual to assume that a parasite which destroys a pest in millions, and with remarkable thoroughness over a given area, is most beneficial. In this particular case, however, such an assumption is entirely unsound. In the absence of the mite, *P. reichei* is, for the most part, a rare and local insect, its multiplication being controlled by its indigenous Hymenopterous enemies, but the presence of the mite makes a pest of an otherwise rare insect. In view of these facts the mite must be regarded, not as a beneficial parasite, as it appears to be at first sight, but as an extremely harmful and undesirable one.

*P. ventricosus* is, in short, the key to the economic aspects of the *Promecotheca* situation in Fiji, except that it is not concerned in multiple-stage outbreaks which, however, are mostly of small dimensions. A full understanding of its activities in outbreaks is therefore essential, and it is convenient here to follow the course of a typical one-stage outbreak from its commencement, with special reference to the mite.

The operations of the mite begin in multiple-stage outbreaks and at the beginning of the dry season. It is immaterial whether the pest covers only one tree, or a small group of trees, or very many trees, the only requirement being that the pest should be abundant. So long as *P. reichei* is rare, it does not serve as a host for the mite, but as soon as it becomes crowded in one tree, or in a few adjacent trees, the mite can utilise it as a host and multiply rapidly, provided the crowding occurs during the dry season so that the mite is not hampered by rain. In these circumstances, the mite has everything in its favour initially. All the stages which it attacks are simultaneously and continuously available, and it can therefore breed without interruption; and since its egg capacity is about 90 and an average generation covers 11 days, each individual mite can give rise indirectly to about 700,000 in a month, assuming that all the offspring find food. The rate of development of *P. reichei* is so slow by comparison that no great change in its population takes place in a month. Consequently, even allowing for extensive mortality among the mites through the inability of some of them to find food, the mite population greatly exceeds the *Promecotheca* population in each tree in a month. At first the mites are confined to a few mines only, since all the pupae and all the larger larvae of *Promecotheca* each contain sufficient food for large numbers of mites, and when the mite population equals the *Promecotheca* population there is still a high percentage of larvae and pupae unattacked. Very soon, however, the mites are compelled by food shortage to leave the mines in which they were born, and at this time they spread all over the tree in countless thousands. This results in wholesale destruction of 1st, 2nd, and 3rd-instar larvae, and pupae, throughout the tree, and the extent of parasitism in the larvae and pupae reaches almost 100% in about 3 days from the time when the spreading of the mites is first noticeable, and in a week the parasitism is total. The only individuals of *P. reichei* which escape are adults and eggs, and as soon as larvae emerge from the eggs laid before the mite reached its maximum abundance they are all destroyed, the mite population now being enormously in excess of

that of *Promecotheca*. Hence, the only individuals ultimately left are all adults, and these are of various ages. The youngest have about a month to live and have not yet begun ovipositing, and the oldest are dying every day. Oviposition therefore continues for a month, but decreases every day towards the end of the month as the oldest beetles die. The outbreak has now been transformed by the mite into the typical one-stage form, with a maximum difference in age of one month between the youngest and oldest individuals. The Hymenopterous parasite, *E. hispidarum*, which would soon have stopped the outbreak if all stages had continued to be present simultaneously, almost entirely dies out through lack of larvae for food for its progeny. The outbreak is at preseut small and covers only a few trees, or perhaps only a single tree, but it is destined to develop until it covers thousands of trees or perhaps the whole estate or island, and this is due solely to the mite.

For about 2 weeks after they have killed all the larvae and pupae, the mites survive in large numbers by feeding for 2, and often for 3, generations upon the remains of the older larvae and the pupae. When there is no food left in any of the older mines, they again spread all over the tree and find all the young larvae that have resulted from the eggs laid by the beetles. The difference in age between the youngest and oldest pest individuals is now about 2 weeks only.

At this time the mites die in millions. Only young larvae are present, and these are not very numerous and are distributed all over the tree. The vast majority of mites can find no food and die of starvation. The young larvae which are available are not large enough to support more than one or two mites each; and the progeny of these few mites are compelled by food shortage to leave the mines in which they were born, but most of them cannot find new mines because the latter are now very scarce. Therefore, by the time when about half the *Promecotheca* eggs have hatched almost all the mites are dead, and the mite population is once more very much smaller than the *Promecotheca* population, which is itself enormously reduced. The percentage parasitism is consequently very low. Since the beetles are very soon all dead, no further increase in the *Promecotheca* population can occur until the individuals which are now young larvae reach maturity. The comparative rarity of *P. reichei* is therefore maintained for about 3 months and the mites are at a great disadvantage throughout this period. As the larvae grow, the mites can multiply since the progeny of each mite can now feed on the host which their parent killed and fed on, but they cannot overcome the disadvantage of the scarcity of hosts, and this disadvantage increases as the few larvae which they succeed in finding are destroyed. In this first generation of a one-stage outbreak the mites are always rare, and even at the end of it they are difficult to find and the percentage of pupae destroyed is negligible.

At the end of this generation, the mites are faced with a further handicap. Between the time when the last beetle emerges from its mine and the time when the first egg of the next generation hatches a period of about 3 weeks elapses, and during these weeks the mites have nothing whatever to attack except the few larvae and pupae of other species of insects which they find in the trees. The few that succeed in finding

the latest pupae, after most of the beetles have emerged, produce progeny some of which feed on the same hosts. These, in turn, produce progeny, which feed cannibalistically on their parents and on each other. In these ways, the species survives the 3 weeks, but in very small numbers, relatively. Meanwhile, however, the *Promecotheca* population increases very greatly, since almost all the beetles remain within the area in which they emerged, and lay all their eggs therein. The percentage of mites which succeed in finding host individuals increases with the concentration of the host, and when the eggs of this generation hatch the mines are comparatively crowded, and the mites therefore benefit greatly. There is, however, very great disparity in numbers initially between host and parasite, and throughout the periods when 1st and 2nd-instar larvae are present the mites, although multiplying continuously, are strictly limited in their multiplication by the small sizes of their hosts. The 1st-instar larvae, particularly, are often destroyed in very large numbers at this time, especially those which result from the later eggs, but the actual percentage destroyed is small.

Soon, however, the dominant stage of the host is the 3rd instar, and this period is followed by one of pupal dominance. In these two periods the mites multiply with extraordinary rapidity, since each host individual is large enough to support many mites, each of which produces, on the average, 90 offspring. The suddenness of the increase in the rate of multiplication is very noticeable in the field towards the end of the 3rd-instar period; the mite which attacks each host at the beginning of that period produces progeny many of which remain in the mine and feed on the same host, but the progeny of these, at the end of the period, find nothing left to eat in the mine and therefore leave it and swarm all over the leaf in search of new mines. From this time onwards the percentage of host individuals destroyed increases rapidly daily. Many of the earlier pupae escape, and produce beetles in due course, but later all the remaining pupae are destroyed, parasitism reaching 100%. The mites are so excessively abundant that they cannot fail to find every single remaining pupa, but they almost invariably reach this degree of abundance too late to prevent emergence of adults from the earlier pupae, and therefore they can never stop the outbreak.

The important point at this stage is the killing of all the later pupae. In this generation of *Promecotheca*—the second since the outbreak began in one-stage form—there is a tendency for the difference in age between the youngest and oldest individuals to become considerably more than a month, which was the extent of the difference at the beginning,* because the rate of development is not constant for all individuals. Actually, by the time the larvae are full grown, the difference in age amounts to about 5 weeks. The tendency towards the multiple-stage condition is therefore very marked already, and in the absence of abnormal factors only one more generation would be required before almost complete overlapping of generations was established. This condition would be reached during the wet season, and the indigenous Hymenopterous

* The difference in age in the 1st generation is about 2 weeks, but in the 2nd generation the difference is increased to a month because oviposition covers about 2 weeks.

parasites, having all stages of the host constantly available and abundant, and no serious enemies to cope with on account of the adverse effect of the rain upon the mites, would effectively bring the outbreak to an end in the last generation in the wet season. This, however, cannot happen. By killing off all the later pupae of the second generation, the mites greatly reduce the difference in age between the youngest and oldest beetles. They cause the difference to become a fortnight or less, and in most outbreaks it is 10 days only. That is to say, the beetles, instead of emerging over a period of 5 weeks, emerge for 10 days only; after that, no more can emerge because all the remaining pupae are dead. Thus, in the dry season, the mite causes the death of the pest in enormous numbers; but in doing so it enables the pest to continue breeding, without serious interference from the indigenous Hymenopterous parasites, by eliminating the tendency towards overlapping of generations. The pest receives a very severe set-back numerically, but to its own ultimate advantage, and the enormous dimensions which outbreaks ultimately attain are actually due to the destruction of the pupae in thousands at this time.

The wholesale destruction of pupae in the second generation of the outbreak coincides with the end of the dry season. As before, the mites die in millions, since only adult beetles, and their eggs, are present, but this time they have no chance, in normal years, to recover numerically when larvae again appear because of the advent of the wet season. The pest now has all in its favour. Each beetle oviposits for about 12 days (this being the period in the wet season, when the temperature is higher) and then dies, and since the difference in age between the youngest and oldest beetles is 10 days, the total oviposition period covers 22 days, or about 3 weeks, and this is the extent of the variation in age in the resulting larvae. These larvae flourish, there being scarcely any mites now, and almost all of them pupate in due course and eventually yield adults in the middle of the wet season. These adults are excessively numerous, as there was no appreciable mortality in the pupae. The variation in age of the beetles is about one month, the variation in duration of the life cycle being about 1 week, and therefore the eggs which they produce vary in age to the extent of about 5½ weeks; but this variation is immediately reduced to about 3 weeks only by the egg parasite, which pounces upon all the earlier eggs, having by this time (the fourth generation of the pest) become tolerably abundant.* This generation becomes adult after the next dry season has set in, and the difference in age of the beetles is about a month, but before the adults emerge the mites again become active, and the later pupae are all killed, with the result that the difference in age is once more reduced to about 10 days only.

It is not necessary to pursue the history of the outbreak further, as the activities of *P. ventricosus* continue in the manner already described, and the egg parasite (and, to a less extent, *Elasmus*) continues to supplement the action of the mite in limiting the variation in age in each generation of *P. reichei*.

In unusually dry years the mites are very noticeably more numerous. Normally, their activities at those times when 1st-instar larvae are present are, as we have shown, not marked, but if the amount of rainfall is not

* The activities of the egg parasite are described in a later section (pp. 125–8).

sufficient to check them periodically very severely, they become so excessively numerous that the numbers which survive the adult and egg periods are abnormally great and the percentages of 1st-instar larvae destroyed are abnormally high. In these circumstances, also, the period during which the adult beetles emerge in bulk from the mines, before 100% pupal parasitism is attained, may be reduced by the mites to no more than 5 days. Therefore, whenever the dry season is unusually protracted, or the wet season has less rain than usual, the outbreaks develop much more slowly. As a rule, they are not stopped, but the pest population may remain constant until heavy rain falls and enables the pest to multiply again. The damage is postponed by the mite, but is not prevented.

Since *P. ventricosus* is the cause of one-stage outbreaks, and these outbreaks are normally the only ones that do serious damage, the accidental introduction of *P. ventricosus* into Fiji must be regarded as the factor principally responsible for making *P. reichei* a pest. That the mite reached Fiji as a result of the development of trade there can be little doubt, since it thrives upon many insects which feed in stored products, and its introduction throughout the islands in the cargoes of ships would follow rapidly after its introduction into the Group. It probably arrived in Fiji between 1850 and 1900, but any further speculation upon the time of its arrival is useless. The important point is that the arrival of the mite completely disorganised the natural control of *P. reichei*, by preventing the indigenous enemies from suppressing it before it spread and from overtaking it afterwards. At the same time, the extensive cultivation of the coconut palm inland gave *P. reichei* greater facilities for spreading away from these enemies. These two factors, the arrival of the mite and the cultivation of the palm, were jointly responsible for the frequent occurrence of *P. reichei* in outbreak form.

b. *Increase and Spread of the Pest.* Since every one-stage outbreak originates from a multiple-stage outbreak, the extent of defoliation in the trees covered by the latter is already considerable at the time when the one-stage condition commences. The pest population is greatly reduced by the process of conversion to the new condition, but after one generation it is restored to its former dimensions. At the end of the first generation, partial spreading may or may not take place, according to the degree of defoliation, but in any case the infested area is not greatly extended. No extensive spreading takes place for either 3 or 4 generations (usually 4), that is, for a little less or a little more than a year. By this time maximum defoliation and population have been reached throughout the area already attacked, and the spreading which now takes place is of maximum extent and equal in point of distance to that which we have already described for multiple-stage outbreaks. The mode of spreading differs in the two types of outbreak, for whereas in multiple-stage outbreaks the spreading from the original area, having once begun, is continuous, in one-stage outbreaks, the spreading continues for a short time only, namely, the duration of the adult life. In both cases, however, the distance through which the beetles spread is the same, so that although the occupation of the new area in multiple-stage outbreaks is continuous, in both cases the boundary of the new area, having once been established, remains constant.

The suddenness with which the spreading takes place is very characteristic of one-stage outbreaks. It is due simply to the suddenness with which the pest population becomes adult. The most important result of it is that the pest suddenly escapes from its Hymenopterous parasites. Were it to remain wholly within the original area, the egg parasite would destroy all the eggs, and therefore stop the outbreak, after 2 more generations. As it is, the pest suddenly invades new areas which are devoid of parasites, and the adult parasites which follow it are extremely few. In multiple-stage outbreaks, on the other hand, the parasites spread with the pest, since the spreading of the latter is gradual and all stages are constantly present.

In the new area, therefore, the pest can multiply almost at the maximum rate. If the spreading takes place in the dry season, the pest is attacked at once by *P. ventricosus*, which is already in the trees, but the comparative scarcity of mines at first causes the percentage parasitism by the mite to be very low. If the spreading occurs in the wet season, there is ordinarily nothing to hinder the pest. In either case, maximum defoliation is usually reached in the new area in only 2 generations, the initial population having been much greater in this area than in the original one when the outbreak began. At the end of the first of these 2 generations, the damage in the trees is not very noticeable except when specially sought, and consequently severe defoliation occurs comparatively suddenly. On this account, and because the new area is very large by comparison with the old one, residents commonly report that severe outbreaks have very suddenly developed. In reality, the outbreaks reported have been developing for no less than 6 generations (21 months).

Further spreading now takes place, after only 2 generations in the new area, and it takes place exactly as before, and through the same distance. The total area now covered is very large, and many thousands of trees are involved. By this time, however, the egg parasite has usually attained 100% parasitism in the original area, and the outbreak in that area, but not elsewhere, is stopped, after the pest population has remained approximately constant for 2 generations.

From this time onwards spreading to new areas takes place every second generation. The estate may therefore be divided into areas each of which is characterised by the duration of the period of occupation of it by the pest, and these areas are usually very clearly defined. Every time spreading occurs, the pest not only invades a new area but also re-invades the area from which it spread 2 generations previously, but it cannot spread far enough to re-invade the area from which it spread 4 generations previously. The pest population remains constant in any one area for 2 generations after spreading from that area has occurred; then all the eggs are destroyed by the egg parasite, so that no more beetles develop within that area, but for 2 more generations beetles come in from the neighbouring area more recently attacked, and their eggs are all destroyed also.

The great majority of outbreaks develop in exactly the manner which we have described. Not infrequently, however, the normal course is modified slightly by natural barriers, or as a result of unusually slow multiplication of the pest when the mite becomes abnormally active in

very dry weather, or because the transformation from the multiple-stage to the one-stage condition is not effected at the same time in all the areas concerned. This last circumstance has peculiar and interesting consequences, which can best be explained by an example. We will begin with a small multiple-stage outbreak and assume that maximum defoliation is reached in May, so that spreading begins then. The outbreak now covers a considerable area, and this is divisible into two areas A and B, of which A is the original area with a dense pest population, and B is a much larger area, surrounding A, in which the pest population is sparsely distributed and nowhere dense, and no appreciable damage has yet been done. In A, the conditions are ideal for the mite. In B, there are no mines, and the pest is, in any case, much too scarce for the mite's requirements. The beetles continue spreading from A to B, since they are constantly present in A. Suppose, now, that in June (*i.e.* a month after spreading commenced, when dry weather prevails) the mite becomes excessively abundant in A, with its customary suddenness, and causes the one-stage condition. The beetles present in A will lay their eggs and die, and then no more beetles will emerge until October. In B, beetles are present during May, June, and part of July, so that the multiple-stage condition is established. In October, when the beetles appear in A, all stages are present in B, but have not become sufficiently numerous, in the period of one generation, for the mite to exert any appreciable influence. The wet season begins soon afterwards and consequently the mite cannot increase and becomes, in fact, much rarer. At the end of January, beetles again appear in A, the one-stage condition having been maintained by *Oligosita*, and in May still another generation of beetles appears. Meanwhile, the multiple-stage condition prevails in B, but the pest population is now very dense in B, and the dry season has commenced, with the result that in June the mite causes the one-stage condition in B. That is to say, beetles only are present in B when young larvae only are present in A, and from this time onwards there is always a difference of one month between the stages of the pest in A and B. Throughout the further spread of the pest (from B to C, and C to D, and so on) the one-stage condition prevails, so that no matter how many times spreading takes place the stage of the pest is the same throughout the whole of the outbreak area except A.

This phenomenon is somewhat exceptional, but has nevertheless been observed by the writer in 3 separate outbreaks—1 on Munia and 2 on Vanua Balavu. It is exceptional because it can only occur if the one-stage condition is first established soon after spreading has taken place and because the pest is often suppressed by *Oligosita* in the original area before the one-stage condition is established in the second area. When it does occur, however, it is very striking, the dividing line between the two areas being clearly marked. On one side of the line, one stage is present, and on the other side, a totally different stage is present, and yet there is no doubt that the infestation on one side has come from the other side. The phenomenon is, in fact, one of the most striking manifestations of the powerful influence of *P. ventricosus*.

c. *Termination*. The causes of the termination of one-stage outbreaks are *Oligosita utilis*, *P. ventricosus* itself, and abnormal weather conditions.

*Oligosita* is the most usual cause. *Elasmus* appears never to terminate one-stage outbreaks, although it is the principal factor in the termination of the multiple-stage type. Its ineffectiveness in one-stage conditions is due to its inability to survive in large numbers the periods when no larvae of the pest are present, and also to the fact that it is destroyed by *P. ventricosus* to the same extent as the pest itself.

*Oligosita utilis* is severely handicapped, like *Elasmus* but to a less extent, by the long periods during which the stage which it requires (in this case the egg) is absent, and eggs are not present long enough to enable it to pass through more than one generation in each generation of the pest. For these reasons, it does not overtake the pest numerically in any one area until after the pest has spread to other areas. Usually, 6 generations are necessary before it can suppress the pest. Consequently, although the ultimate termination of the outbreak is usually due to *Oligosita*, the termination is only possible when further spreading of the pest is prevented by natural barriers or is delayed because the multiplication of the pest in the most recently infected areas is itself delayed. In no other circumstances can *Oligosita* overtake the pest. On a small estate, therefore, which is isolated from other coconut areas by sea or forest, the termination of an outbreak usually occurs when the whole estate is covered by the pest, but not before. The pest cannot spread further, and *Oligosita* then suppresses it 2 generations later. On large estates, the extent of which is great enough to enable the pest to continue its advance after it has been eliminated by *Oligosita* in the areas which were first attacked, the outbreak is never held np by natural boundaries and unless other conditions change *Oligosita* can never overtake the pest. Such outbreaks can continue for years, and often do so. They are not stopped by *Oligosita* until weather conditions—either excessive rain, affecting the pest directly, or excessive drought, affecting the pest through *P. ventricosus*—cause an abnormal and extensive reduction in the pest population so that the spread of the pest from the most recently infected areas is delayed for 2 generations.

*P. ventricosus*, as we have seen, destroys the pest in enormous numbers in the dry season, but not sufficiently in normal circumstances to stop an ontbreak. When the dry season is unusually protracted, however, the mites become excessively numerous and are occasionally sufficiently abundant, before the end of the last pest generation of the dry season, to kill all the pupae before any adults emerge. The outbreak is then completely stopped, by *P. ventricosus*. More frequently, however, the abnormal abundance of the mite, resulting from exceptional protraction of the dry season, causes the pest population to remain constant, instead of increasing, for 2 or more generations; and in these circumstances spreading is delayed long enough for *Oligosita* to overtake the pest. *Oligosita* stops the outbreak, but the mite enables it to do so.

Abnormal weather conditions are the least frequent cause of the termination of outbreaks. Rainfall is the factor principally concerned. If heavy rain, accompanied by gales, falls for many days, either without stopping or stopping for short periods only, at the time when 1st-instar larvae are present, heavy mortality by drowning results and the pest population is so greatly reduced that the outbreak is virtually stopped.

It is possible that this factor sometimes completely destroys all the larvae, but in any case further spreading is delayed sufficiently long to enable *Oligosita* to effect complete suppression of the pest. It should be noted that, whereas at least 2 periods of exceptional rain are required to check multiple-stage outbreaks, 1 is sufficient to check one-stage outbreaks.

d. *The Duration and Extent of the Predominance of each Stage.* These matters were studied at Nabavatu in 1933, in an area in which a severe outbreak was raging. The outbreak had begun about 5 generations previously, and in May, when these observations commenced, the dominant stage was eggs. From May to October, sample leaflets were taken at least twice a week from the centre of this area, and the number of living individuals of each stage was recorded on each occasion. In this way it was possible to ascertain when each stage first appeared and when it finally disappeared, and also the period during which each stage predominated (*i.e.* was more numerous than any other stage). The results, which are typical of all one-stage outbreaks in the dry season, are tabulated below :—

*Table VI.*

| Stage. | Present. | Predominant. | |
|---|---|---|---|
| Eggs . . . | May 6–June 18 | May 14–June 5 | (22 days) |
| 1st-Instar . . | June 4–July 10 | June 6–June 25 | (19 ,, ) |
| 2nd ,, . . | June 20–Aug. 2 | June 26–July 18 | (22 ,, ) |
| 3rd ,, . . | July 6–Aug. 29 | July 19–Aug. 10 | (22 ,, ) |
| Pupae . . . | July 26–Sept. 4 | Aug. 11–Aug. 22 | (11 ,, ) |
| Adults . . . | Aug. 15–Oct. 10 | Aug. 23–Sept. 10 | (18 ,, ) |
| Eggs . . . | Sept. 4– ? | Sept. 11– ? | |

These data are represented in Fig. 11, in which the thick lines are the periods of predominance and the thin lines passing through the thick ones are the total periods during which the various stages were present. The 6 stages, eggs, 1st instar, 2nd instar, 3rd instar, pupae, and adults are represented by E, I, II, III, P, and A, respectively.

The most important points revealed by these data are :—

(1) Each of the first 4 stages predominated for about 3 weeks.

(2) The pupal stage predominated for 11 days only, owing to the wholesale destruction of all the later pupae by *P. ventricosus*. (Healthy pupae were present until 4th Sept., but were extremely rare from 22nd Aug. onwards.)

(3) The period which elasped between the first appearance of eggs and the first appearance of newly-hatched larvae was 29 days, although the incubation period at this time of year is about 15 days only. The discrepancy was due to the destruction of all the earlier eggs by *Oligosita*.

(4) 1st-instar larvae became predominant only 2 days after they first appeared. That is to say, bulk hatching occurred with remarkable suddenness. The reason for this was that total parasitism by *Oligosita* in the eggs ceased suddenly and then the percentage parasitism decreased rapidly, owing to rapid increase in the number of

eggs present while the *Oligosita* population remained constant or decreased.

(5) *Only the 1st instar became predominant rapidly. All other stages increased in numbers gradually, and the increase was more gradual in the 3rd instar and pupal stages than in the earlier stages because of variation in rate of growth. In the adult stage, the increase again became more rapid because of the sudden destruction of all the later pupae by P. ventricosus.*

(6) The overlapping is such that there can never be more than 3 stages present at any time, and there are often only 2.

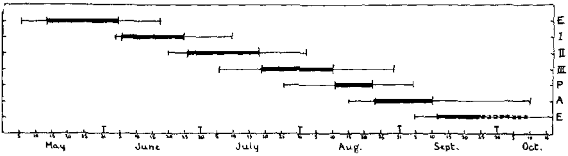



FIG. 11.—Diagrammatic representation of one generation of *P. reichei* in a one-stage outbreak, showing period of presence and period of predominance of each stage. (For further explanation see text.)

*The extent of the predominance of the various stages at different times is illustrated in the table below, in which the number of individuals of the predominant stage on each occasion, and for the sample leaflets taken, is given as a percentage of the total number of living individuals :—*

*Table VII.*

| Date. | No. of Living Individuals. | | | | | | Total Living. | Pre-dominant Stage. | Percentage in Pre-dominant Stage. |
|---|---|---|---|---|---|---|---|---|---|
| | Eggs. | 1st Instar. | 2nd Instar. | 3rd Instar. | Pupae. | Adults. | | | |
| July 4 | — | 18 | 117 | — | — | — | 135 | 2nd Instar | 87% |
| ,, 26 | — | — | 33 | 63 | 1 | — | 97 | 3rd ,, | 65% |
| Aug. 1 | — | — | 14 | 227 | 36 | — | 277 | ,, ,, | 82% |
| ,, 2 | — | — | 17 | 307 | 67 | — | 391 | ,, ,, | 78% |
| ,, 5 | — | — | — | 166 | 88 | — | 254 | ,, ,, | 65% |
| ,, 16 | — | — | — | 47 | 97 | 12 | 156 | Pupae | 62% |
| ,, 29 | — | — | — | 3 | 15 | 81 | 99 | Adults | 82% |

All the figures obtained during this generation of the pest were tabulated in this way, and the seven occasions represented in the above table are typical examples. *It was found that in the middle of the period of* predominance of each stage, the individuals in that stage were usually between 80% and 90% of the total living (except in the period of pupal predominance, when the extent of predominance was at *no time* so high on account of the brevity of the period caused by *P. ventricosus*).

e. *Effect of Natural Barriers.* The inability of the beetles to cross areas devoid of coconuts has already been discussed, and it is only necessary here to consider the general effect of such barriers on outbreaks.

Every outbreak, if it continues long enough, reaches a stage when the

pest disappears in one area as it invades another some distance away. The disappearance and invasion take place at opposite boundaries of the total area occupied by the pest at the time. Hence, if an outbreak occurs in a locality where the coconut trees are confined to a coastal belt, so that the pest can only spread in one or two directions, the outbreak as a whole shifts periodically along the coast, always in the same direction, or in two parts in opposite directions. On islands which are almost entirely covered with coconuts but on which the coconut areas are partially separated by belts or patches of forest, the same effect is noticeable although less regular. Natural boundaries prevent uniform spreading in all directions and cause the pest to follow a definite course, and consequently the outbreak as a whole shifts from place to place and may move all over the island, even causing re-infection of areas which it defoliated 2 or more years previously and in which the trees have partially recovered in the meantime.

Where there are no natural barriers, the pest tends to spread outwards in concentric rings of equal width. It occupies not more than 4 rings at any one time and is concentrated mainly in the two intermediate ones. The total area attacked tends to increase in size as the diameter of the rings increases, but the width of the area remains constant. Where there are natural barriers, however, such as the sea on one side and wooded hills on the other, so that spreading must take place mainly in one direction, the width of the occupied area is the same as when spreading is in concentric rings but the size of the area remains approximately constant as the outbreak moves.

### 6. The Outbreaks on the Islands Naitauba and Rabi.

We have already had occasion to refer to the fact that outbreaks on Naitauba are very restricted as compared with those of other islands in Northern Lau, and that outbreaks on Rabi are abnormally severe and frequent for an island which is not in Lau.

Naitauba is similar in size, elevation, structure, climate, and the extent to which it is planted with coconuts to the other islands in Northern Lau; *P. reichei* is present on it and so are all the usual natural enemies, and small, negligible, outbreaks, of both the one-stage and the multiple-stage type, occur on it occasionally. Yet, it is unique among the islands of Northern Lau in that no extensive outbreaks have ever been known to occur on it. The principal reasons for the apparent immunity are that Naitauba is comparatively seldom visited by natives from other islands, and that nearly all the boats which call there anchor a long way off the shore. The island is privately owned and there are no native villages, and it is comparatively isolated and not on the routes of inter-island travel within the Lau Group. In these circumstances, the accidental introduction of individuals of *P. reichei* from other islands is a very rare occurrence. Nevertheless, the immunity of Naitauba is apparent rather than real, and is largely attributable to good fortune. Normally, outbreaks which become extensive arise from small ones in which the condition of maximum defoliation is reached at the beginning of the dry season, and so long as the small outbreaks remain infrequent the chance of this condition being reached at this particular time is small. But there

is no immunity on this account, and had not the pest been suppressed throughout Fiji by the introduction of parasites from Java in 1933. severe outbreaks would have been certain to occur at Naitauba sooner or later.

The island Rabi is in the wet zone of Fiji and has a mean annual rainfall of approximately 144 ins., and no long periods of drought. This rainfall is sufficiently great to prevent extensive one-stage outbreaks comparable to those of Lau, and it always does prevent them; yet the outbreaks which do occur are rather more extensive and frequent than would be expected. Unfortunately, the reasons for this were never ascertained, as no detailed study of the pest on Rabi was made, and no investigation of any kind was ever made in the dry season, which is the critical time. It was, however, ascertained that all the usual natural enemies are present, and that the conditions are intermediate between those of one-stage and multiple-stage outbreaks. Some of the coconut areas in which the outbreaks occur are very isolated, being surrounded by high hills and wide stretches of uncultivated land, and it seems probable that this lack of continuity may be concerned with the extent of the outbreaks.

## V. THE NATURE AND EXTENT OF THE CONTROL EXERCISED BY THE PARASITES AND OTHER FACTORS, PRIOR TO 1933.

The factors concerned in the control of *P. reichei*, prior to the introduction of parasites from Java in 1933, were :—

*Oligosita utilis.*
*Elasmus hispidarum* (in conjunction with which it is necessary to consider the secondary parasites, *Tetrastichus taylori* and the Eupelmids).
*Pediculoides ventricosus.*
Predators.
Rain.
The condition of the trees.
Overcrowding.

### A. *Oligosita utilis.*

When each generation of the pest begins in a one-stage outbreak, all the individuals of *O. utilis* are necessarily adults, and all of them are females very eager to lay, the males having died some time previously. As soon as the first eggs appear on the leaves, the parasites pounce upon them, and at first, for some days, the parasitism is always 100% for this reason. But the number of eggs present increases rapidly day by day, while the number of parasites remains constant, and there always comes a time when the rate at which the eggs are laid is greater than the rate at which they can be attacked by the parasites, and from that time onwards, so long as oviposition by the pest continues at the same or a greater rate, 100% parasitism is impossible and the percentage decreases continuously. Eventually, however, oviposition by the pest reaches its maximum; and then it declines until, finally, no more eggs are laid because all the beetles are dead. This decline gives the parasites once more an opportunity to increase the extent of parasitism, and if they can live long enough and in sufficient uumbers 100% parasitism is again possible, although actually it is but rarely attained. The parasites, being already old at the commencement of the period of oviposition, die in large numbers before the end of it, and only a small percentage survive to attack the eggs laid towards the end of the period. The parasite population decreases steadily throughout the period of oviposition. Thus, *O. utilis* (like *E. hispidarum*) is considerably handicapped by the lack of any overlapping of generations of the pest. It is this factor which is mainly responsible for the inability of the parasite to check the pest appreciably before the latter reaches the stage of maximum population.

On account of its long life cycle the parasite is incapable, in normal circumstances, of passing through more than one generation in each

generation of the pest, for the adult parasites cannot begin to emerge until long after the last of the host eggs has hatched. Repeated observations in the field showed that *O. utilis* usually begins to emerge, from the earliest *Promecotheca* eggs, at the time when the majority of the healthy individuals of the pest have just reached the 2nd instar, and that it continues to emerge for almost exactly a month and ceases when the majority of healthy individuals have reached the 3rd instar and some have pupated. Therefore, as a rule, even the earliest *Oligosita* have no eggs left to attack (see fig. 11), and it is certain that all of these earliest individuals die without ovipositing, as no more host eggs are laid until about 10 weeks later, this being the time between the beginning of the period of 2nd-instar dominance of one generation and the beginning of egg-laying in the next generation. The latest *Oligosita* individuals, however, have to wait not longer than 5½ weeks, and most of them can survive this period. It is these latest individuals which pounce upon the first eggs laid in the next generation and cause, temporarily, 100% parasitism, but although large numbers survive until the first eggs appear, they are only a small percentage of all those that emerged from the previous generation of eggs of the pest.

In certain circumstances, however, a partial, but negligible, second generation of *Oligosita* occurs in one generation of the pest. It often happens, for reasons explained elsewhere, that the stage of the pest in newly-infested areas is different from that in the original area which was the source of infestation. In such cases, some of the beetles from the newly-infested area occasionally migrate to the original one after all those in the latter have died, thereby lengthening the period during which eggs are present. All the eggs laid by the immigrants are then available to the earliest *Oligosita*, which normally would have none at their disposal, and a partial second generation takes place. Parasitism in the eggs laid by the immigrants invariably reaches 100%, so that no additional overlapping of generations of the pest results from the invasion.

It has already been pointed out that at the beginning of the period when eggs are present, parasitism is 100% for some days. The number of days during which all the eggs are parasitised by *Oligosita* is small at first, but is usually about 15 in outbreaks that have been in progress for 4 generations or longer. After these 15 days, the rate of oviposition by the pest is so rapid that the parasites which are still alive cannot cope with it, and the percentage parasitism rapidly falls. The destruction of all the earliest individuals for 15 days is always very evident in the field. Eggs of the beetles appear comparatively suddenly on the trees, and it is always possible to see when oviposition begins in bulk. Ordinarily, an observer would then calculate that the first mines would appear 15 days later, since the incubation period covers 15 days (in the hot season). But this does not happen. The mines do not appear until about 30 days later, on account of the activities of *Oligosita*. In other words, the observed life cycle in the field, of the pest in bulk, from the beginning of the egg-laying period of one generation to the beginning of the corresponding period of the next, which averages 102 days in the hot season, is about 15 days longer than the actual life cycle (from egg to egg), and this apparent lengthening is due largely to *Oligosita*. Another result,

frequently observed in the field, of the activities of *Oligosita*, is that the eggs of the pest begin to hatch in enormous numbers with extraordinary suddenness. One day no new mines are apparent in the trees. On the next day new mines, varying in age up to 24 hours, are abundant in every tree. The eggs themselves appear in bulk suddenly, but not nearly so suddenly as this, and the explanation of the sudden hatching is that in the earlier part of the egg-laying period *Oligosita* kills all the eggs as they are laid, but every day the number of eggs increases very greatly while the number of parasites decreases, and eventually the time comes when the rate of laying exceeds the rate of destruction, and this time must necessarily come suddenly. Consequently, hatching commences with corresponding suddenness, the incubation period being nearly constant.

Statistics obtained in 1929 and 1933 will serve to illustrate the extent of the control exercised by this parasite in typical one-stage outbreaks. At Nabavatu, in 1929, the pest generation which began in July showed an average parasitism for the whole estate of 25%. In November, when the eggs of the next generation of the pest were laid and the condition of maximum defoliation had been reached almost everywhere, the average parasitism for the whole estate amounted to 44%, and in certain areas where the outbreak was of long standing the percentage reached 100. Hence, the average parasitism increased from 25% to 44% in one generation and was almost total locally; but by this time, as is always the case, very great damage had been done to the trees, and although *Oligosita* undoubtedly reduced the rate at which the pest spread, it did not succeed in preventing it from spreading over the whole estate. The parasite postponed the damage, but did not ultimately lessen it, and the reason for its failure was that it was unable to spread as rapidly as its host. In 1933, also at Nabavatu, the parasitism in the area in which the outbreak had begun was 16% in June and 40% in the next generation in October; and the pest spread as rapidly as in 1929 and would certainly have covered the whole estate again had it not been completely controlled in 1934 by parasites introduced from Java. On other islands (Kanacea and Mago) similar percentages were noted.

Since, in one-stage outbreaks, the pest spreads periodically, not continuously, every estate is divisible into areas characterised by the ages of their outbreaks, and in each area the percentage parasitism depends upon the age of the outbreak in it. In newly-infested areas the percentage is low, and in areas where the pest has long been established it is high. The average for the whole estate at any one time rarely exceeds 50%, but in each area a maximum of not less than 80% is reached 2 or 3 generations after the pest has spread from that area while maintaining its population therein, and usually the percentage reached is 100. It was always noticed that the percentage is approximately doubled at each successive generation of the pest, and that either 6 or 7 generations are ordinarily required before maximum parasitism is attained. The parasitism at the beginning of an outbreak in any area to which the pest suddenly spreads is usually about 2% in the first generation, and in the next 5 generations, provided the area is not excessively exposed to the wind, it is approximately 5%, 10%, 20%, 40%, and 80%; but since the pest

usually spreads after 4 generations, having attained maximum population, the maximum parasitism is reached much too late.

In coastal areas which face the trade winds, or high inland areas which are constantly wind-swept, parasitism by this species reaches, but rarely exceeds, 60%, and therefore outbreaks in such places often continue, though not iu very severe form, for abnormally long periods. In individual trees growing actually on the sea-shore and fully exposed to the wind, *O. utilis* is often rare, while in neighbouring trees a short distance inland it is abundant; the pest, on the other hand, is usually most abundant in the most exposed trees, and this is undoubtedly due in part to the effect of the wind on this parasite, but an equally important factor is the tendency of the pest to congregate in the most exposed trees.

It is now necessary to consider the activities of the parasite in the conditions which lead up to multiple-stage outbreaks. The pest is initially rare and complete overlapping of generations prevails. The parasite can breed continuously, since some eggs are always available for it, but it is greatly handicapped by their rarity and its own minute size and fragility. The eggs in each tree are not concentrated on one leaflet but are distributed irregularly throughout the tree, and since each tree bears about 6,000 leaflets, which are almost constantly lashed by the wind, the chances of the parasite finding the eggs are remote. In these circumstances parasitism is usually about 5%, and rarely more, and not infrequently the parasite is entirely absent. The pest, in uou-outbreak condition, is always very unevenly distributed on any island, and the parasite is consequently even more unevenly distributed. The former is liable to increase locally, still in multiple-stage condition, anywhere, but whether the increase takes place in a locality in which the parasite has managed to snrvive the previous rarity of its host is purely a matter of chance. The parasite can always survive on all islands, except the smallest, but it cannot survive in all localities. *Elasmus*, on the other hand, is always present, in the writer's experience, and when the pest multiplies at the beginning of a multiple-stage outbreak, *Elasmus*, on account of its much shorter life cycle, can take advantage of the greater abundance of the host more rapidly than *Oligosita*, even when the latter is present initially. By the time that the pest becomes really abundant, *Elasmus* is much more plentiful than *Oligosita* and usually stops the outbreak, unless *P. ventricosus* intervenes, before *Oligosita* has had sufficient time to affect the pest population greatly. *Oligosita* helps to accelerate the suppression of the pest, but *Elasmus* is the main factor concerned, although in one-stage conditions *Elasmus* is peculiarly useless. *Oligosita* can multiply much more rapidly in multiple-stage conditions than in one-stage conditious and is capable of suppressing an outbreak in which the former prevail, but the presence of *Elasmus* renders it unnecessary.

## B. *Elasmus hispidarum.*

In one-stage outbreaks, *E. hispidarum* can multiply throughout the period when *Promecotheca* larvae are available and it can pass through 3 generations in one of the pest, or roughly one per instar of the pest. Moreover, since the adult life is long compared with the period of the life

cycle and oviposition is continuous during the adult life, all stages of the parasite are present after one generation and breeding is absolutely continuous. To this extent, conditions are favourable for the parasite. At the end of each generation of larvae of the pest, however, the parasite inevitably receives a severe check. Only pupae are available, and they are useless to it. Moreover, they are followed by adults and eggs, which are equally useless. The period during which no larvae are present covers about 6 weeks. The great majority of the parasites fail to survive this long period and die without progeny. Only those which result from the last of the larvae can survive, and if it were not for the very long adult life, the species could not survive at all in one-stage outbreaks. As it is, a few survive, and these pounce upon the young larvae of the next generation as soon as they appear, but these surviving parasites have not much longer to live and their oviposition period is consequently quite abnormally short, as is readily observed in the field by the sudden disappearance of the eggs of *Elasmus* soon after the young larvae of *Promecotheca* have begun to appear. The result is that *E. hispidarum* is set back in every generation of the pest.

The lack of any overlapping of generations of the pest is therefore a very serious obstacle to this parasite; and the parasite itself helps to prevent any overlapping, to its own detriment, by attacking the first larvae to appear at the beginning of each generation and the last to become full grown.

The multiplication of the parasite is further greatly hindered in outbreaks by the activities of the natural enemies already noted and by the death of its larvae in large numbers as a result of the premature decay of the hosts and of the frequent failure of the parent parasites to paralyse the hosts.

These factors together cause the parasite to be entirely ineffective economically in one-stage outbreaks. It is found, in each generation of the pest, to be no more common than in the previous generation.

Statistics obtained at Nabavatu will serve to illustrate the impotence of *Elasmus* in one-stage outbreaks. In 1929 a very severe outbreak covered the whole estate. The activities of *Elasmus* were carefully watched and checked numerically by the method described in Section IX. The following results, beginning in July when the predominant stage of the pest was 1st instar, were obtained :—

*Period when 1st Instar predominant (July–Aug.).*

| | |
|---|---|
| Total no. of mines examined (from 6 localities and 14 trees) . . . . . . . . . . | 2,106 |
| Total no. of mines attacked by *Elasmus* . . . . . | 76 |
| Percentage attacked by *Elasmus* . . . . . . | 3·6 |

*Period when 2nd Instar predominant (Aug.).*

| | |
|---|---|
| Total no. of mines examined (from 6 localities and 11 trees) . . . . . . . . . . . | 1,692 |
| Total no. of 1st and 2nd-instar mines attacked by *Elasmus* | 119 |
| Percentage attacked by *Elasmus* . . . . . . | 7·0 |

*Period when 3rd Instar predominant (Aug.–Sept.).*

| | |
|---|---|
| Total no. of mines examined (from 5 localities and 9 trees) | 1,701 |
| Total no. of 1st, 2nd, and 3rd-instar mines attacked by *Elasmus* | 72 |
| Percentage attacked by *Elasmus* | 4·2 |

*Period when Pupae predominant (Sept.).*

| | |
|---|---|
| Total no. of mines examined (from 6 localities and 12 trees) | 6,298 |
| Total no. of 1st, 2nd, and 3rd-instar mines attacked by *Elasmus* | 264 |
| Percentage attacked by *Elasmus* | 4·2 |

These figures show clearly that the percentage destroyed by *Elasmus* was almost negligible throughout this generation of the pest, being in the neighbourhood of 5% only, although the outbreak had been in progress for about 2 years. Actually, there was a slight increase in the percentage, which does not appear clearly in the figures, towards the end of the generation, as the activities of *Elasmus* are cumulative throughout the larval stage, but the increase was negligibly small because enormous numbers of the parasites were destroyed by *Pediculoides* and *Tetrastichus*.

In 1933, also at Nabavatu, similar figures were obtained. The outbreak had been in progress for more than one year. The percentages destroyed by *Elasmus* were worked out exactly as in 1929, with the following results (all from the same locality, but on different trees) :—

*Period when 1st Instar predominant (June).*
Percentage attacked by *Elasmus* = 2·7 (12 in 449).

*Period when 2nd Instar predominant (June–July).*
Percentage attacked by *Elasmus* = 4·9 (41 in 842).

*Period when 3rd Instar predominant (July–Aug.).*
Percentage attacked by *Elasmus* = 5·2 (7 in 135).

*Period when Pupae predominant (Aug.).*
Percentage attacked by *Elasmus* = 7·0 (79 in 1,133).

*Period when 1st Instar again predominant (Oct.).*
Percentage attacked by *Elasmus* = 2·9 (44 in 1,532).

These data support those obtained in 1929, and they show clearly the increase in the percentage destroyed by *Elasmus* as the generation of the pest progresses, the negligible extent of the parasitism in spite of this increase, and the return at the beginning of the next generation to a smaller percentage which is scarcely greater than that of 4 months earlier. At the end of the June–Aug. generation, the beetles spread enormously and were infinitely more abundant than in the previous generation. *Elasmus* exercised no appreciable check upon them.

It must be borne in mind, in estimating the population or the multiplication of this parasite, that it is not sufficient to estimate only the per-

centage of mines attacked. The stage of the mines must also be considered. Thus, in the figures given for 1933, 2·7% of the mines were attacked in the 1st-instar period, and since there is usually only one parasite in each 1st-instar mine, this means that for every 100 mines there are 2·7 parasites. In the 3rd-instar period, the percentage of mines attacked was 5·2, but some of these were 1st instar, some 2nd, and some 3rd, and the number of parasites per mine is 2–6 in 2nd instar and 6–18 in 3rd. The number of parasite individuals per 100 mines is therefore much greater than 5·2 and is probably approximately 15, and the figures for both 1929 and 1933, while showing only a slight increase in the number of pest individuals destroyed in one generation, definitely show a considerable increase in the parasite population when all stages of the parasite are included.

Hitherto we have been considering only the effect of one-stage outbreaks on this parasite. In islands or localities where the pest is present in multiple-stage condition, the parasite is definitely of value. In such circumstances, *E. hispidarum*, with or without *Oligosita utilis*, is an efficient check upon the pest; and so long as other factors remain unchanged it is able to breed without interruption and to maintain with the pest an equilibrium such that no extensive outbreak can occur. This equilibrium is not constant, but wave-like, and when the pest is at the crest of a wave a small, localised, outbreak results. All stages of the pest are still present simultaneously, and *Elasmus* is usually able to overtake the pest numerically, attaining 100% parasitism, in time to prevent the outbreak reaching serious dimensions. As a general rule, 100% parasitism is attained about 9 months after the pest has first begun to multiply. These small outbreaks are inherent in the normal equilibrium between parasite and host, and it is only when the equilibrium is disturbed by *Pediculoides* or hurricanes, which are factors entirely outside the normal scope of *Elasmus*, that an extensive outbreak can occur. In all other circumstances, *Elasmus* preserves a satisfactory equilibrium, and although it may be condemned for its uselessness in one-stage outbreaks, its existence definitely renders severe outbreaks of all kinds much rarer than they would otherwise be, and this is a valuable service. Its chief utility lies in the fact that it suppresses many of the small, normal, outbreaks before they can be transformed into one-stage outbreaks by *Pediculoides*.

Hurricanes cause severe outbreaks of *P. reichei* by eliminating this parasite temporarily in areas where it was previously maintaining a satisfactory equilibrium. The outbreaks which result are very extensive. They may even be comparable in extent to the typical one-stage outbreaks of Lau, but they differ in that all stages are present at the same time. Their serious nature, due as it is to the absence of *Elasmus*, is a striking demonstration of the usefulness of *Elasmus* in ordinary circumstances.

In one-stage outbreaks, natural enemies, though not the main factor concerned, render *Elasmus* more ineffective than it would otherwise be. *Tetrastichus taylori* always maintains a parasitism of not less than 40% in *Elasmus* in all one-stage outbreaks of the pest, and a parasitism of 60% is not uncommon locally. *Elasmus* is therefore severely hampered

by this hyperparasite, the effect of which is continuous throughout each generation of *Promecotheca*.

In multiple-stage outbreaks, the pest is controlled by *Elasmus* in spite of the presence of *Tetrastichus*. The reason for the failure of *Tetrastichus* to multiply more rapidly appears to be that each *Elasmus* individual is subject to the attack of the secondary parasite for a short time only in the course of its development. This, together with the inevitable initial discrepancy in numbers, hinders *Tetrastichus* continuously, while *Elasmus* has nothing to hinder it.

The two Eupelmid species are of no economic importance as secondary parasites of *P. reichei*. The percentage of *Elasmus* destroyed by them is always very small and negligible, even in outbreaks of long standing. It is almost certain that these Eupelmids have many alternative hosts, though none is actually known, and this would account for their rarity as enemies of *Elasmus*. In any case, they could never destroy a very high percentage of *Elasmus* because they cannot destroy all the *Elasmus* individuals in large, 3rd-instar, mines, and because cannibalism almost invariably prevents the continued existence of more than one Eupelmid individual in any one mine.

### C. *Pediculoides ventricosus*.

*P. ventricosus* is active only in the dry season, and the extent of its activities depends largely upon how long it has to wait, after the beginning of the dry season, before the conditions which it requires for rapid multiplication prevail. It can multiply rapidly only when large larvae and pupae of the pest are present. If these stages are present when the dry season begins it can multiply immediately, and consequently, at the beginning of the larval period of the next generation it is present in considerable numbers, in spite of very heavy mortality during the intervening period when only adults and eggs of the pest are available. As the larvae of this next generation grow, the mite multiplies increasingly, until, when large larvae and pupae again become available, it exerts its maximum effect. If, on the other hand, the predominant stage at the beginning of the dry season is adult beetles, the mite must wait for about 3 months until conditions become ideal for its multiplication, and then, before another generation of larvae can become full grown and pupate, the wet weather usually begins and the mite is reduced by it to a condition of great rarity. In the former case, therefore, conditions are favourable for the mite in two successive generations of the pest, whereas in the latter case they are favourable for one generation only.

The Nabavatu outbreak of 1929 afforded an instance of the maximum destruction of the pest by the mite. Eggs were predominant in July, when the dry season was already well advanced, and the resulting adults were predominant in October. Throughout this period, sample leaflets were taken regularly from all parts of the outbreak area where the pest had reached its maximum abundance, and records were kept of the total number of eggs of this generation laid on the samples taken, and also of the number of living individuals of each stage and of the number which had been destroyed by *P. ventricosus* and other causes, separately. The statistics obtained during each period of predominance were added to-

gether and the totals thus obtained for the 6 months are tabulated below :—

*Table VIII. Illustrating Progressive Destruction of* P. reichei *by* P. ventricosus.

| Total Eggs on Leaflets Examined. | Healthy Eggs. | Healthy 1st Instar. | Healthy 2nd Instar. | Healthy 3rd Instar. | Healthy Pupae. | Healthy Adults. | Total Living. | Percentage Living. | Total destroyed by Mites. | Total (except eggs) destroyed by other Factors. | Percentage of hatched Individuals destroyed by Mites. | Dominant Stage. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 691 | 371 | 112 | — | — | — | — | 483 | 70 | 8 | 5 | 6·4 | Eggs |
| 3,441 | 266 | 1,526 | 93 | — | — | — | 1.885 | 55 | 411 | 76 | 19·5 | 1st Instar |
| 2,484 | 2 | 84 | 576 | 117 | — | — | 779 | 31 | 796 | 119 | 47·0 | 2nd ,, |
| 2,475 | 0 | 9 | 176 | 317 | 26 | — | 528 | 21 | 1,101 | 72 | 64·7 | 3rd ,, |
| 3,379 | 0 | 0 | 0 | 104 | 344 | 84 | 532 | 16 | 1,690 | 97 | 72·8 | Pupae |
| 955 | 0 | 0 | 0 | 1 | 9 | 80 | 90 | 9 | 485 | 35 | 79·5 | Adults |
| I | II | III | IV | V | VI | VII | VIII | IX | X | XI | XII | |

In column VIII the total number of living individuals present (including healthy eggs, if any) is shown. The figures in this column are of no significance in themselves, since the number of samples varied in the different periods, but when expressed as percentages of the numbers of eggs originally laid, they are very significant (column IX). They show that the percentage of healthy individuals of the pest decreased steadily from 70% at the time when eggs were dominant to 9% when adults were dominant. At the time when eggs were dominant, a few 1st-instar larvae were already present, and 6·4% of these were destroyed by the mite. The fact that only 70% of the individuals were living at this early stage was due largely to the egg parasite, but from this time onwards the rapid decrease in the percentage living was due almost entirely to the mite. The only other destructive factor operating was *Elasmus*, but very few individuals were destroyed by it (column XI). Column X shows the number of individuals destroyed in, and prior to, each period by *P. ventricosus*, and in column XII the figures in column X are expressed as percentages of the number of eggs which hatched (*i.e.* of the number of individuals present when the ravages of the mite commenced). The number of eggs which hatched is obtained by summing the figures in columns III, IV, V, VI, VII, X, and XI. The percentages in column XII, therefore, represent the rate of destruction of the pest by *P. ventricosus* alone, and it is clear that the percentage destroyed increases rapidly in each period, until, at the end of the generation, 79·5% of the individuals which hatched have been destroyed. Actually, the total destroyed amounted to even more than 79·5% because the observations on which Table VIII is based ceased when the adults first became predominant and while healthy pupae were still present and available to the mite. The total destroyed by the end of the generation was therefore determined in the manner detailed below.

In the periods when pupae and adults predominated, the numbers of individuals already killed by the mite were 1,690 and 485 respectively (Table VIII). The 1,690 consisted of 1,459 killed as larvae, 219 as pupae,

and 12 as adults in their mines; and the 485 consisted of 463 killed as larvae, 15 as pupae, and 7 as adults in their mines.* The numbers of eggs which had hatched in the sample leaflets taken during these two periods were 2,319 and 610 respectively (Table VIII), making a total of 2,929, and the total number of larvae killed by the mite was 1,922 (1,459 + 463). Hence,

$$\text{Percentage of individuals killed as larvae by mites} = \frac{1{,}922 \times 100}{2{,}929}$$
$$= 66\% \text{ (approx.)}$$

In addition, *Elasmus* killed 4% of the larvae in this generation of the pest, and therefore 30% became pupae. In order to ascertain what percentage of those which became pupae were attacked, sooner or later, by mites, a large number of sample leaflets were collected at the time when no living pupae were left, and the fate of every individual which reached the pupal stage was recorded. In this way, the following data were obtained :—

| | | |
|---|---|---|
| Pupae killed by mites . . . . . . | 889 | 1,091 |
| Adults destroyed in mines by mites . . . | 202 | |
| Adults which emerged from their mines . . | 513 | |
| Total . . . | 1,604 | |

Hence, percentage of prepupae, pupae, and adults killed by mites

$$= \frac{1{,}091 \times 100}{1{,}604}$$
$$= 68\% \text{ (approx.)}$$

Thus, although 30% of the larvae survived to pupate, 68% of these survivors were ultimately destroyed. This means that 20% (68% of 30%) of the larvae originally present were killed as prepupae, pupae, and adults. The total number of individuals destroyed by the mite therefore amounted to (66 + 20)%, that is, 86% of the total number of larvae which were originally present.

Destruction of the pest amounting to between 80% and 90% is typical of all outbreaks in normal years, provided the generation concerned begins late enough in the dry season for the mite to be numerous at its commencement.

If a pest generation begins when the dry season itself begins, the mite remains extremely rare until large larvae or pupae are present. In 1933, 4 separate outbreaks (3 on Vanua Balavu and 1 on Kanacea) in which a generation began at the beginning of the dry season were investigated from time to time. The percentage mortality due to mites was very low as compared with that observed in other outbreaks which occurred at the same time but in which the corresponding generation began later. In these 4 outbreaks, the percentages of the hatched

* Only the sums of these figures are shown in Table VIII.

individuals destroyed by mites in the sample leaflets taken were approximately as follows :—

| | | |
|---|---|---|
| In the period when eggs predominated | . | 0·0% (0 in 1,328) |
| ,, ,, ,, 1st Instar ,, | . | 0·3% (1 in 403) |
| ,, ,, ,, 2nd ,, ,, | . | 1·0% (7 in 697) |
| ,, ,, ,, 3rd ,, ,, | . | 1·1% (29 in 2,643) |
| ,, ,, ,, Pupae ,, | . | 10·0% (35 in 344) |
| ,, ,, ,, Adults ,, | . | 33·0% (528 in 1,604) |

These figures show that *P. ventricosus* remained rare and made no appreciable progress until the pest individuals reached the pupal stage. The mite then multiplied very rapidly, and by the time when adults predominated it had killed 33% of the total number of individuals which hatched. The 33%, however, consisted largely of the later individuals, and parasitism in the individuals which remained in their mines did not become total until about 2 weeks after emergence of the adults had begun. The outbreak was not greatly checked, but the one-stage condition was maintained.

As a parasite of *Elasmus. Tetrastichus*, and the two Eupelmids, *P. ventricosus* is formidable. It enters all mines equally readily, regardless of their contents, and it attacks the parasites and hyperparasites of *P. reichei* as readily as it attacks *P. reichei* itself. The numbers of each species of parasite and hyperparasite destroyed are therefore proportional to the numbers of *P. reichei* destroyed, and the percentages are equal. When the mites become abundant at the end of each dry-season generation of *P. reichei*, the parasitism of *Elasmus, Tetrastichus*, and the Eupelmids by the mite is almost total if the parasitism of *P. reichei* by it is itself almost total. Thus, the mite hampers the Hymenopterous parasites very severely, but only in the dry season, and only in the sense that it reduces the parasite population to an extent such that the ratio between the pest and parasite populations remains constant. In the wet season, being very scarce, it does not attack the parasites appreciably and they become more numerous, but *Elasmus* is still hampered by its inability to survive in large numbers the long periods when no larvae of *P. reichei* are present, and *Tetrastichus* and the Eupelmids, being dependent on *Elasmus*, are correspondingly hampered. The mite is the principal cause of the lack of larvae during these long periods, and it hinders the parasites more by causing this periodic lack than by killing a very high percentage of them in the dry season.

As a parasite of *O. utilis*, the mite is rare and negligible, because it can only enter a parasitised egg of *Promecotheca* through fractures in the under surface of the chorion, and fractures very rarely occur.

## D. Predators.

The predatory animals which attack *P. reichei* are ants and lizards. The mode of attack in each case has already been described, and we shall refer here only to the extent to which the pest is destroyed.

The attack of ants (principally *Monomorium floricola*) upon the eggs of *P. reichei* is fairly consistent in all outbreaks and localities. The

number of eggs destroyed is high, but on account of the enormous number of eggs present the percentage destroyed is low. In individual trees, however, the percentage is occasionally very high. In the outbreaks at Nabavatu in 1929, 7% * of the eggs were destroyed by ants, and this low percentage included eggs on trees in which ants were exceptionally active, the trees and leaflets used as samples being chosen entirely at random by a native. The percentage appears never to exceed 10 over a wide area.

The attack of ants upon larvae and pupae in mines is much less constant, although it is due to the same species. Occasionally, the percentage of larvae and pupae destroyed is high over considerable areas, but this appears to occur only in very dry weather, and then only locally. The attack of ants upon mines cannot therefore be included as a normal controlling factor.

Lizards never devour the eggs, but are occasionally responsible for wholesale destruction of the large larvae and pupae. The activities of lizards in this respect, however, are very erratic and local, and they do not appreciably affect the course of an extensive outbreak. Moreover, lizards appear to attack *P. reichei* extensively only in periods of extreme drought, although, having begun, they are usually extremely thorough, destroying about 50% of all the larvae and pupae in the trees concerned, aud 80% in some of the leaves. As enemies of the adult beetles lizards are negligible.

### E. Rain.

In normal years, raiu is not a controlling factor in any way. Exceptionally long periods of wet weather, however, particularly if the rain is heavy and driven by strong winds, occasionally causes almost complete destruction of the pest by drowning and consequently causes the termination of outbreaks, but this happens so rarely that it cannot be regarded as within the normal natural control. The reasons for the comparative rarity of this occurrence are, first, that extensive drowning only results when heavy rain continues, without sunny intervals, for a period of not less than 30 hours, and this is a comparatively unusual circumstance in Fiji; and secondly, that only 1st-instar larvae are easily drowned. Consequently, extensive drowning takes place only when 1st-instar larvae predominate; and unusually wet weather seldom happens to coincide with a period of 1st-instar predominance.

There is a very prevalent belief in Fiji that the wet season is detrimental to the pest. This is due to the fact that the damage done in severe outbreaks is always most noticeable in the dry season. The truth of the matter is that the majority of severe outbreaks are one-stage outbreaks, and in one-stage outbreaks the pest population is very greatly reduced by *P. ventricosus* at the end of the dry season. In the wet season, therefore, the pest is much less numerous at first and the damage is correspondingly less.

* The total number of eggs on the leaflets examined, after the time when all the healthy eggs had hatched, was 12,734, and the number destroyed by ants was 891, or 7%. Eggs which had been parasitised and were attacked by ants subsequently were not included in the 891.

### F. The Condition of the Trees.

In unhealthy trees, 1st-instar larvae (but no other stages) die in large numbers in their mines, sometimes to the extent of 90%. The poor state of health of the trees may be due to unsuitable soil conditions, in which case the death of the larvae occurs locally only, or to abnormal drought, in which case the death of the larvae is general. These two causes affect the larvae in the same way. The tissues bordering the mines in unhealthy trees become callused abnormally rapidly and the veins are abnormally tough, with the result that young larvae cannot obtain an adequate food supply.

Large numbers of 1st-instar mines which are surrounded by bands of hard, dead, tissue, and contain dead larvae are a common sight upon the leaves in certain localities at all times, and in other localities in periods of drought. In these cases, the dead tissue is usually the direct cause of death, but in most localities this factor rarely arises, and it cannot be included within normal control.

### G. Overcrowding.

Overcrowding is a common cause of the death of larvae of *P. reichei*, but it accounts for only a small percentage in most outbreaks. When the pest is prevented from spreading and is confined to a small group of trees by natural barriers, overcrowding is liable to occur and to result in heavy mortality; in large areas overcrowding is a negligible factor, although a few dead larvae whose death is undoubtedly due to it can usually be found in most leaves. The condition of maximum defoliation is reached without appreciable overcrowding. After this time, the number of eggs laid greatly exceeds the number of larvae for which the supply of green tissue is sufficient, but a high percentage of eggs is usually destroyed by this time by *Oligosita* so that the number of larvae is not excessive. The meeting of mines is very seldom a cause of mortality, although it very frequently appears to be. Mines in contact with one another and containing dead larvae are often common, but if observations are made at the time when such deaths occur, it is usually found that death is due to other factors, which happen to operate when the mines meet. The larvae are very seldom prevented from feeding by an obstruction at the normal point of feeding. Except in the 1st instar, the larvae are able to resume feeding with ease at any point along the sides of their mines, so that they can avail themselves of the green tissue in all directions if necessary. The most common causes of mortality which arise in circumstances such that death appears to be due to the meeting of mines are *P. ventricosus* and the dying of surrounding tissue in dry weather. After maximum defoliation has been reached, the number of mines on any one of the older leaves very greatly exceeds the number of larvae which one leaf can nourish. The mines, however, represent many generations and most of them are old. A large proportion of them are small, their larvae having died as a result of attack by *P. ventricosus* and *Elasmus* in previous seasons. The number of eggs laid by one generation of beetles on such leaves is nearly always proportional (roughly) to the amount of green

tissue left. If all the eggs and small mines present contained living individuals at the same time, very heavy mortality would result from overcrowding; but since they represent many generations, and the beetles, when ovipositing, are controlled by the mines already present, overcrowding causes the death of a negligible percentage only.

### H. The Combined Effects of the Various Factors.

Three of the factors which cause the death of the pest in large numbers operate locally and occasionally only. These three are rain, the condition of the trees, and overcrowding, and they cannot be included in a general estimate of the natural control. The other four factors are the natural enemies, and these usually operate on all islands and in all localities, and therefore constitute the normal natural control.

The outbreak at Nabavatu in 1929 was used to ascertain the extent of the control due to natural enemies. In the generation which began with eggs in July, sample leaflets were taken at regular intervals from all the areas in which maximum defoliation had been reached, and in this way an average estimate for the whole estate was obtained. The outbreak was of the one-stage type, and all the natural enemies were probably exerting their maximum influence in the dry-season generation in which the observations were made. No controlling factors, other than natural enemies, had any appreciable effect on the pest in this generation.

The percentages of the pest destroyed by the various natural enemies have already been stated separately, and they may now be summarised here as follows :—

| | | |
|---|---|---|
| Percentage of eggs destroyed by *Oligosita* . . . | 25 | 32 |
| ,, ,, ,, ants . . . . | 7 | |
| ,, larvae ,, *Elasmus* . . . | 4 | 90 |
| ,, ,, (including later stages) destroyed by *Pediculoides* . . . | 86 | |

Thus, only 10% of the individuals which were not destroyed as eggs escaped the attack of natural enemies later, and since 68% of the eggs hatched, the few individuals which eventually emerged from their mines as adults amounted to only 7% (10% of 68) of the total number of eggs originally laid, 93% having been destroyed by natural enemies alone.

This very low percentage emergence is typical of any dry-season generation in which the mite has been able to begin multiplying at the very beginning of the dry season. In all dry-season generations, however, the combined activities of the natural enemies cause a high percentage destruction and the percentage of eggs which eventually produce adults never exceeds 20. In the wet season, on the other hand, the percentage of eggs which produce adults is comparatively high, and it is probably not less than 60 on the average for the whole of any outbreak area, though no actual counts were made. Thus, although the natural enemies may destroy 93% in the one complete generation in the dry season, the mean percentage destruction for the 3·5 generations in the year is not particularly high. Moreover, even though only 7% of the eggs produce adults, the pest receives only a temporary check. We have already seen

that the number of beetles produced per tree per generation when maximum defoliation is reached is, in the absence of controlling factors other than *Oligosita*, about 4,000. Assuming that the average destruction of eggs by *Oligosita* is 25%, these 4,000 result from about 5,300 eggs. If, then, 7% of the eggs produce adults when the natural enemies are all exerting their maximum influence, the number of beetles produced per tree is in the neighbourhood of 370 (7% of 5,300). In the following generation, which matures in the wet season in the absence of mites, the destruction by natural enemies is small and the pest multiplies greatly, with the result that the population per tree again approaches the maximum. Alternatively, we may consider that 100 eggs are laid by 5 females and that approximately 5 males are present also, the total population being about 10. From the 100 eggs, 7 beetles eventually result, so that although the population is not increased, it is not very greatly decreased.

## VI. THE SEARCH FOR PARASITES FOR THE CONTROL OF *P. REICHEI*, THE HISPIDS AND PARASITES CONCERNED, AND THE SELECTION OF PARASITES.

### A. The Hispids most likely to yield suitable Parasites.

Species of Hispid beetles occur in almost all tropical countries, and in many they are plentiful. They feed principally upon monocotyledonous plants. Their larval habits vary greatly: some feed externally in exposed positions upon the leaves; others feed externally but in sheltered positions, living between adjacent leaflets of young, unopened leaves, or inside rolled leaves; others again feed inside the leaves as true miners. The true miners include species which leave their mines to pupate and also species which (like *P. reichei*) pupate within their mines.

In almost all countries there are certain parasites which attack a great variety of insects, even attacking species which mine in leaves occasionally. These parasites are always very rare and erratic as enemies of leaf-miners and obviously cannot be expected to play any part in the natural control of the latter. All leaf-miners are also attacked, however, by certain parasites which feed upon no other insects. The leaf-mining habit is an extremely specialised one, and if the parasite is to subsist solely upon leaf-miners, its own habits must become extremely specialised also. Thus, a parasite which commonly attacks a Hispid which does not mine cannot be expected to serve as a control for a mining Hispid which is completely concealed from it. But the specialisation must in some cases be carried much further than this, for although in some countries leaf-miners are present in a number of different plants, in many localities they are present in only one or only a few plants, and can only be found by intensive searching amongst a great variety of vegetation. A parasite, therefore, if it is to avail itself to the full of the supply of leaf-miners, must develop the habit of frequenting certain plants, and this is particularly true in the case of the coconut palm, whose habitat and mode of growth are such that its leaves form a roof high above other vegetation. Insects which feed upon it are partially protected from parasites which chiefly frequent plants near the ground and are liable to be attacked commonly only by species which have acquired the habit of frequenting coconuts only or coconuts and certain other plants equally. Thus, although a parasite which normally frequents other plants might conceivably attack a leaf-miner in coconut more commonly in the absence of the other plants, it would be much less likely to serve as an effective control than one which normally frequents coconuts.

For these reasons, there was little hope of obtaining parasites for the control of *P. reichei* from any Hispid other than the comparatively few species which mine in coconut leaves. Even amongst the parasites of

these latter Hispids, the prospects of finding one which could be expected to flourish in the very special conditions prevailing in Fiji outbreaks did not seem good. Comparatively few parasites of coconut Hispids were known, and those which were known did not appear to be any better suited for the control of *P. reichei* than the parasites already present in Fiji. The only initial course to pursue, however, was to investigate the parasites of closely allied coconut Hispids thoroughly. The genus *Promecotheca* itself includes several species which mine in coconut leaves and whose habits are very similar in most other respects to those of *P. reichei*. The genus is represented in Malaya, the East Indies, China, the Philippines, Australia, New Guinea, the Solomon Islands, the New Hebrides, and Fiji, but its geographical centre appears to be the Far East, as is the case with many other similarly distributed genera of insects. On this account, and because the parasite fauna of the Far East was likely to be richer and more varied as regards habits, than that of countries nearer to Fiji, the most hopeful sources of parasites appeared to be Malaya, the East Indies, and the Philippines. The species of *Promecotheca* which mine in coconut leaves in these countries are *P. cumingi* (Malaya, Borneo, and the Philippines), *P. soror* (Moluccas), and *P. nuciferae* (Java and Celebes). These three are extremely closely allied, and it seems probable that they are better regarded as geographical races of the same species.

The indigenous parasites in Fiji were already known to be capable of controlling *P. reichei* in the multiple-stage condition, which is the normal and inevitable condition. The damage done by *P. reichei* is due almost entirely to the one-stage condition which is wholly outside the normal scope of the parasites and is due to an abnormal, introduced, factor. This condition effectively prevents the parasites from exerting their normal controlling influence. Its maintenance is due partly to *P. ventricosus* and *O. utilis* and partly to the fact that the oviposition period of *P. reichei* is very short as compared with the total life cycle. During the wet months of the year, the mite does not operate, and if the oviposition period of the pest were longer, complete overlapping of generations would result and the indigenous parasites would stop outbreaks before the operations of the mite began again. The same reasoning would apply to any other Hispid, and consequently no Hispid which occurred in persistent one-stage form could be expected to yield parasites which could control *P. reichei*. The available information concerning other Hispids was very scanty, but it sufficed to indicate that *P. cumingi* and *P. nuciferae* always occur in multiple-stage form and can never occur in one-stage form, their oviposition periods being very long as compared with their life cycles. Had one-stage outbreaks of these Hispids been known to occur, the investigation of their parasites for the control of *P. reichei* would have been useless; as it was, there was at least some hope of obtaining suitable parasites from them. Incidentally, it is noteworthy in this connection that the natural control, by indigenous parasites, of a Hispid which can occur only in the multiple-stage condition could never be improved upon by the introduction of parasites obtained from one which occurs in the one-stage condition, but the reverse introduction would not necessarily be useless.

## B. The Search for Parasites in Java.

The search for parasites for the control of *P. reichei* was commenced in Java in 1930 by R. W. Paine, who made a preliminary survey of the parasites of *P. nuciferae.* Paine, at that time, was principally engaged upon a study of *Tirathaba* spp. and was not able to devote much time to *Promecotheca*, but he nevertheless succeeded in obtaining 6 species of parasites (including 2 secondaries) and in amassing a considerable amount of information concerning their bionomics and relative importance. This information proved most useful subsequently as a basis for the detailed investigation carried out by the present writer during the whole of 1931 and part of 1932. Moreover, the latter investigation showed that, although *P. nuciferae* is occasionally attacked by a few species of parasites other than those found by Paine, there are no others which play any appreciable part in the control of that insect. Paine's investigations were conducted mainly in the neighbourhood of Poerwaredjo in Central Java.

In 1931, eggs and mines of *P. nuciferae* were collected from a very large number of localities in West, Central, and East Java. The centres from which the search was conducted were Buitenzorg in the West, Poerwaredjo in Central Java, and Malang and Djember in the East. Material from 38 different localities, representing almost the whole country, was thus obtained. The towns in the neighbourhood of which the most extensive collections were obtained were Batavia, Anjer Lor, Tjileungsir, Tjiamis, Keboemen, Poerwaredjo, Singasari, Gondanglegi, Poeger, and Banjoewangi. Since *P. nuciferae* is, on the whole, a rare and local insect in Java, the collection of material was a most tedious process, and not infrequently careful searching for several days with the assistance of natives yielded only a few dozen eggs and mines. Occasionally, however, localities in which the insect was more plentiful were found, and the material eventually obtained was ample for experimental purposes as well as for judging the relative utility of the various parasites.

The Hispid fauna of Java is comparatively rich, and attention was paid to the parasites of many other Hispid species besides *P. nuciferae* because it was considered necessary to obtain some knowledge of the alternative hosts, if any, of the parasites of that insect, although no new parasites which might be obtained from other Hispids could be expected to be useful. The majority of Hispids in Java are leaf-miners, but there are others—on coconuts as well as other plants—which do not mine but feed superficially. Many plants which abound in most parts of the country are attacked by various species of Hispids, and these plants include bamboo, rice, banana, and zingiberaceous species. The collection of other Hispids was therefore not difficult, but since almost all of the species found proved to be very local in most instances it was not possible to obtain much material at any one time.

Attention was chiefly paid to Hispids which are to be found between sea-level and about 1,500 ft.; that is, within the normal range of *P. nuciferae.* Hispids abound locally, however, in the mountain forests, up to an elevation of about 5,000 ft., feeding principally on plants of the families Zingiberaceae, Musaceae, Commelinaceae, and Gramineae, and some of these were investigated, principally on Mt. Gedeh in West Java.

In the earlier stages of these investigations in Java, it was anticipated

that a search in other countries also might prove desirable, notably in the Moluccas, Celebes, and the Philippines. As the work in Java progressed, however, it became evident that at least one of the Java parasites promised to be suitable for the control of *P. reichei*, and it was therefore decided not to undertake any further search before testing the Java species. Subsequently, one of the Java parasites proved completely successful, and the search therefore never extended further than that island.

In addition to Hispid mines, the mines of a Buprestid, *Aphanisticus latus*, Kerr., and of 2 species of Tineid moths of the genus *Cosmopteryx*, which were the only other insects found in Java mining in coconut leaves, were collected to ascertain whether any of the parasites of *P. nuciferae* attacked them also.

## C. The Parasites of *P. nuciferae* in Java, and their alternative Hosts.

The parasites obtained in 1930 by R. W. Paine from *P. nuciferae* were :—

*Dimmockia javanica*, Ferr.
*Pleurotropis painei*, Ferr.
,, *parvulus*, Ferr.
,, *detrimentosus*, Gahan
*Achrysocharis promecothecae*, Ferr.
*Achrysocharella orientalis*, Ferr.

Of these, all except *P. detrimentosus* were previously unknown. *A. orientalis* and *P. detrimentosus* are secondaries, and the other four species are primary.

In addition to these, three other parasites * were found in 1932 attacking *P. nuciferae*. These were :—

*Polysphincta* sp., an Ichneumonid.
*Opius* sp., a Braconid.
*Cirrospilus* sp., a Eulophid.

These three species are all primary parasites. Thus, 7 species of primary parasites and 2 species of secondary parasites were obtained from *P. nuciferae* in Java. Of the 7 primaries, *D. javanica*, *P. parvulus*, and *A. promecothecae* are abundant as parasites of *P. nuciferae*, and are almost invariably present together wherever their host occurs; the other 4 primaries are very rare as parasites of *P. nuciferae*. *D. javanica* is an external parasite of the larva, attacking all the larval instars equally readily. *P. painei* is an internal parasite of the pupa only. *P. parvulus* is an internal parasite of all the larval stages and of the pupa. *A. promecothecae* parasitises the egg. *Polysphincta* sp., *Opius* sp., and *Cirrospilus* sp. are larval parasites. *P. detrimentosus* and *A. orientalis* attack *D. javanica*, *P. painei*, and *P. parvulus* as internal parasites.

No Hispids, other than *P. nuciferae*, were found mining in the leaves

* Specimens of all these parasites have been submitted to the British Museum for determination but the specific names are not yet available.

of coconuts in Java. There are, however, 3 species, *Botryonopa sanguinea*, Guer., *Bronthispa longissima*, Gestro, and *Plesispa reichei*, Chap., which feed between adjacent leaflets in the unopened leaves. These are attacked by several species of parasites, but they are never attacked by any of the species which parasitise *P. nuciferae*.

The Hispids found mining in the leaves of bamboo were *Downesia excelsa*, Spth., *D. perniciosa*, Spth., *D. sumatrana*, Gerst., *Agonia pallipes*, Spth., and *Agonia opacula*, Spth. These are all attacked by the same parasites. Eight different species of primary parasites, of which one attacks the eggs and the other 7 attack the larvae and pupae, were obtained from these bamboo Hispids. In addition, 2 species which are possibly secondary were also obtained. The egg parasite was *A. promecothecae*, which attacks *P. nuciferae*. Of the larval and pupal parasites, 4 species (*P. painei*, *Polysphincta* sp., *Opius* sp., and *Cirrospilus* sp.) attack *P. nuciferae* also; these 4 species are all very rare as parasites of bamboo Hispids, and are equally rare as parasites of *P. nuciferae*. The other 3 species of larval and pupal parasites were never found to attack *P. nuciferae*; two of them were reared only from bamboo Hispids, while the third, which was abundant as a parasite of the latter, was occasionally reared also from *Gonophora xanthomelana* in banana. Neither *D. javanica* nor *P. parvulus* was ever reared from bamboo mines, nor was either of the 2 secondary parasites of *P. nuciferae*.

In addition to the Hispids that mine in bamboo leaves, there is a species (*Leptispa bicornis*, Spth.) which feeds, as a larva and as an adult, superficially on bamboo leaves, living concealed in a tube which is formed by the longitudinal rolling-up of the leaves, from their edges inwards. The rolling of the leaves results from the death and the drying of the tissues along the edges where the Hispid attacks them, and the larva is provided with a long, rigid, anal process, bifurcated terminally, which projects upwards at right-angles to the body and apparently serves to prevent the leaf from rolling too tightly. This process, unlike somewhat similar processes in other Hispid larvae, is not associated with the tracheal system. It was thought that this Hispid, whose habitations, though not true mines, correspond to the mines of other species, might be attacked by some of the parasites of the true miners, and a large number of the rolled leaves were collected from several localities to test this possibility. It was found, however, that this species is never attacked by any of the parasites of any true miner, whether of bamboo, coconut, or any other plant investigated. Only one species of parasite was obtained from it, but this one, which attacked the larvae and pupae, was very abundant.

*Gonophora xanthomelana*, which mines in bananas, orchids, and zingiberaceous plants, yielded 9 species of primary parasites and 2 secondaries. Four of the 9 primaries were obtained only in the mountains. They were obtained, not only from *G. xanthomelana*, but also from *G. taylori*, Spth., in *Amomum* leaves, *Prionispa fulvicollis*, Guer., in leaves of *Pollia thyrsiflora* (Commelinaceae), and an unidentified Hispid in the leaves of a Musaceous plant. Two of the remaining 5 primaries were obtained at low levels only and attacked Hispids mining in bamboo, but not in coconut. The other 3 primary parasites were obtained in the mountains and at low levels also; they were *P. painei*, *P. parvulus*, and

*A. promecothecae*, all of which attack *P. nuciferae*. but whereas all of them were found abundantly as parasites of *G. xanthomelana* and also of *G. taylori*, only 2 of them, *P. parvulus*, and *A. promecothecae*, commonly attack *P. nuciferae*. The 2 secondary parasites of *G. xanthomelana* were *P. detrimentosus* and *A. orientalis*. *D. javanica*, *Polysphincta* sp., *Opius* sp., and *Cirrospilus* sp. were never obtained from *G. xanthomelana*.

*Hispa wakkeri*, Zehnt., *H. armigera*, Oliv., and several other species which mine in the leaves of rice and other grasses, did not yield any of the larval or pupal parasites which were obtained from *P. nuciferae*, although they proved to be attacked by some of the species obtained from bamboo. Their eggs, however, were attacked by *A. promecothecae*.

The mines of the Tineids in coconuts yielded 2 species of parasites, but neither of these was obtained from any Hispid. *Aphanisticus latus*, Kerr., yielded 3 species, 2 of which were obtained from no other host, while the third was *Cirrospilus* sp. which attacks *P. nuciferae* and bamboo Hispids rarely.

In addition to the Hispid species that have already been mentioned, several other species were investigated for parasites, but there is no need to discuss these here as the details already given serve our present purpose, which is to show that most of the parasites of Hispids in Java have many hosts, and that nearly all those of *P. nuciferae* attack other Hispids also.

Laboratory tests showed that nearly all the parasites which were never obtained from *P. nuciferae* in the field would attack the mines of that insect in captivity. It was also found, in all cases, that it is the mine, not the contained insect, which attracts the parasite in the first place, empty mines being as attractive as others. Further tests showed that most of the parasites of mining Hispids would attack individuals of Hispids such as *Plesispa* spp., which do not mine, if these were placed inside mines from which the normal occupants had been removed, and this was found to apply in the case of the secondary parasites as well as the primaries. Other experiments showed that the common parasites of *P. nuciferae* would attack the mines of *Aphanisticus latus* in coconut very readily and would oviposit therein, but their progeny could not mature in this host. From these experiments with *A. latus* it was inferred that the parasites of *P. nuciferae* attack *A. latus* in the field also, showing no discrimination between the mines of the two insects when these occur together in the same trees. The attacked individuals of *A. latus* are killed, but the parasites die with them. Thus *A. latus* must be almost completely exterminated in any locality where individuals of *P. nuciferae*, and therefore of its parasites, are plentiful. Since the reverse probably applies also, it follows that *P. nuciferae* and *A. latus* cannot both be plentiful at the same time in the same locality, but both can be present simultaneously in a state of comparative rarity in the same locality. This conclusion agrees with field observations.

From this general survey of parasites and hosts the following conclusions were drawn :—

i. The parasites of mining Hispids do not attack Hispids which do not mine and vice versa.

ii. The parasites of mining Hispids may be classified into 2 groups;

first, those which frequent one species of plant only, and secondly, those which frequent two or more species; the selection of hosts depending upon the plant or plants frequented by the parasites, rather than upon the species of host.

iii. When several species of Hispids mine in the same plant species, the parasites which frequent the latter not only attack all the Hispids but also can mature in all of them. If a mining insect of another family or order is present also, the parasites may attack it, but often cannot mature in it.

iv. Some of the parasites (*e.g. P. painei* and *Polysphincta* sp.) which frequent several species of plant, do not often ascend far above the ground and therefore do not often attack Hispids in coconuts, although, having found the latter, they attack them readily and can mature in them.

v. Some parasites that attack a great variety of insect species occasionally attack mining Hispids, but cannot properly be regarded as Hispid parasites.

As far as the parasites of *P. nuciferae* are concerned, this general survey led to the following conclusions :—

i. *D. javanica* frequents coconuts only, and is consequently a parasite of *P. nuciferae* only. (A very closely allied species of *Dimmockia* was found attacking *G. xanthomelana* in bananas and also the bamboo and rice Hispids, but it was never obtained from *P. nuciferae*.)

ii. *P. painei* frequents bamboo and the food-plants of *G. xanthomelana*, but rarely visits coconuts. It operates mainly near the ground.

iii. *P. parvulus* frequents coconuts and bananas equally, as well as the other food-plants of *G. xanthomelana*, but does not frequent bamboo or other Gramineae, although it can develop in Hispids in these latter plants when induced in the laboratory to attack them. (The question of host-selection by *P. parvulus* is discussed on p. 202.)

iv. *A. promecothecae*, the egg parasite, frequents coconuts, bananas, Zingiberaceae and Gramineae; in fact, it appears to attack the eggs of all mining Hispids.

v. *Polysphincta* sp., *Opius* sp., and *Cirrospilus* sp. frequent many different plants, but were very rarely obtained from any Hispid. (Very little is known concerning these 3 species, but it is most probable that they have a very wide host range and only occasionally attack mining insects.)

vi. The two secondary parasites frequent coconuts and bananas equally, but do not frequent bamboo or other Gramineae.

vii. Nearly all the parasites of other mining Hispids, including those whose normal habitat is mountain forests at elevations above the normal range of *P. nuciferae*, will attack *P. nuciferae* in the laboratory and can mature as parasites of it. The fact that only 3 species of Hispid parasites, out of the very large number present in Java, attack *P. nuciferae* commonly is in most cases attributable, not to inherent specificity in host-selection by the parasites, but rather to the fact that *P. nuciferae* lives in palms far above the ground, in a habitat peculiar to itself.

## D. The Bionomics of *Promecotheca nuciferae*, Maulik.*

(Plate XX.)

The habits of *P. nuciferae* in all stages are very similar to those of *P. reichei*, and it is therefore only necessary here to refer to the few points of difference which do exist.

The egg is laid singly on the underside of the leaflets of the coconut palm and of a few other palms, but, unlike that of *P. reichei*, it is sunk into the tissues. The female, when about to oviposit, bites out the leaf tissues so as to make an oval, flat-bottomed, cavity, the bottom of the cavity being the upper epidermis of the leaf. The dimensions and outline of the cavity correspond to those of the egg, so that when the egg is laid it fits the cavity closely. After laying the egg, the female covers it with excrement, forming a capsule similar to that of *P. reichei*, but since the top of the egg is nearly flush with the leaf surface, the capsule is only slightly convex and does not project far above the surface, and is consequently much less conspicuous than that of *P. reichei*. There is always a narrow furrow in the leaf extending for a short distance from the end of the egg between adjacent veinlets, the furrow and the longer axis of the egg being in a straight line and parallel to the veins. The furrow is identical with the normal adult feeding-scars and the making of it appears to be a necessary preliminary to the excavation of the cavity. The beetle begins feeding in the usual way, but very soon proceeds to widen the furrow so as to make the egg cavity. In the case of *P. nuciferae*, there is no elaborate process of shaping and smoothing of the excrement with the legs. The beetle merely distributes the excrement by lateral oscillatory movement of its abdomen, but it does not turn round during the process or use its legs for any purpose except gripping the leaf.

The habits of the larvae, including the number of moults, are identical with those of *P. reichei*, except that when the egg hatches, the young larva has no occasion to penetrate the epidermis of the leaf to reach the parenchyma since it is already at the required level while it is within the egg. The mines are approximately of the same shape and dimensions as those of *P. reichei*, and pupation takes place within them.

The habits of the adults of *P. nuciferae* are, in general, similar to those of *P. reichei*. *P. nuciferae* is equally slow and lethargic in its movements, and its flight is equally weak. The method of feeding, the feeding-scars, and the method of emergence from the mine are identical. There are, however, certain important and conspicuous differences, in addition to the difference in the mode of oviposition, and these are enumerated below :—

i. *P. nuciferae* does not drop from the leaves when disturbed.

ii. It is not markedly gregarious at any time during its life.

iii. It is only slightly susceptible to light stimuli.

iv. It does not choose only the most exposed trees and the most exposed leaves for feeding purposes, but feeds equally on all leaves and on all trees, regardless of degree of exposure. This is associated with the lack of susceptibility to intensity of illumination.

*** The larva, pupa, and adult of *P. nuciferae* have been described by Maulik in *Bull. Ent. Res.* 20 : 81, 1929.**

v. It feeds and oviposits very readily, both in the field and in captivity, upon young seedling palms whose leaves have not yet split into leaflets, and the larvae mature in such leaves. The leaves of seedling palms are fatal to *P. reichei* and are never attacked by it in the field.

The most important differences between the two species, however, particularly from the point of view of biological control, are in the rate of development, the duration of adult life, and the egg-capacity. The life cycle was studied at Buitenzorg in March, April, and May, 1932. Sixty individuals were used, all being reared from eggs which were marked as soon as they were laid; half of these individuals were left in the leaves of the seedling palms on which the eggs were laid in cages, and the rest were removed from their original mines at the beginning of the 2nd instar and were then inserted artificially into leaflets from old trees by the method described in Section IX. The experiments were conducted in a shed with open sides, into which the sun penetrated in the early morning and the late afternoon. Both methods of treatment of the larvae yielded exactly the same results, which are summarised below :—

*Table IX. Life Cycle of* P. nuciferae.

(The figures are days to the nearest quarter.)

| Period. | Range. | Mean Duration. |
|---|---|---|
| Incubation . . . . . . . . | 13 –16¾ | 15 |
| 1st-Instar Feeding Period . . . . . . | 3¼– 4¾ | 4 |
| 1st Resting Period (including 1st moult) . . | 1¼– 4 | 2¾ |
| 2nd-Instar Feeding Period . . . . . . | 2¼– 5 | 3¾ |
| 2nd Resting Period (including 2nd moult) . . | 2½– 4¼ | 3¼ |
| 3rd-Instar Feeding Period . . . . . . | 5¾– 8¼ | 6¾ |
| Prepupal Period . . . . . . . | 3¼– 5 | 4 |
| Pupal Period . . . . . . . . | 10¾–12¾ | 11½ |
| Adult Resting Period, spent in Mine . . . | 2 – 3 | 2¾ |
| Total (oviposition to emergence from mine) . | 50 –57½ * | 54¼ * |

* These figures are obtained, not by adding the figures above them, but from the totals for all of the 60 individuals.

The resting period of the larva after each of the two moults and before it resumes feeding varies from ½ to 1¼ days, the mean being ¾. The two resting periods may therefore be divided into a pre-moulting period of 2 and 2½ days respectively and a post-moulting period of ¾ day in each case.

The life cycle may be expressed more simply in the following manner :—

| | | |
|---|---|---|
| Incubation Period . . . . . . . . | 15 days | (mean) |
| Larval Period (including prepupal) . . . . | 24¾ ,, | ,, |
| Pupal period (including period spent by adult in mine) . . . . . . . . . | 14½ ,, | ,, |
| Total . . | 54¼ ,, | ,, |

At the time when these observations were made the weather was hot. In cooler weather, an appreciable lengthening occurs in the duration of each stage, and the total period is approximately 62 days, but this was ascertained for 3 individuals only.

Comparing the life cycle of *P. nuciferae* with that of *P. reichei* in the hot season, we find that :—

i. The development of *P. nuciferae* is very much more rapid than that of *P. reichei.*

ii. The range in the total duration of the life cycle is approximately the same.

iii. The incubation periods are the same in the two species, and the pupal and prepupal periods are almost the same. The difference in rate of development therefore lies almost wholly in the larval periods, and the larval period of *P. reichei* (approximately 39 days, excluding the prepupa) is almost twice as long as that of *P. nuciferae* (approximately 21 days). Expressing these larval periods as percentages of the total periods from oviposition to emergence from the mine, we find that the figure for *P. reichei* is 53%, while that for *P. nuciferae* is only 38%.

Even greater differences are found in the period of adult life, and these are the reverse of those found in the period from oviposition to emergence in that the adult life of *P. nuciferae* is very much longer than that of *P. reichei.* It was not practicable to observe the adult life and activities of a large number of beetles, because each pair had to be kept separately in very large cages containing young palms * planted in soil in tins, and in these circumstances the inspection and attention, at least twice daily for many weeks, were lengthy processes. Records were obtained, however, for 12 pairs in 2 batches, 6 cages (6 ft. × 3 ft. × 3 ft.) with wire-gauze sides being used for the purpose. In these cages, the beetles paired and behaved apparently normally in every way. Of the 12 female beetles, 1 was destroyed by ants after it had begun to oviposit, 2 died after they had oviposited for about 2 weeks through injuries received while they were being transferred to new palms, and the remaining 9 lived and oviposited normally. The records obtained are summarised in Table X below.

*Table X. Adult life of* P. nuciferae.

(The figures are days.)

| Period. | Range. | Mean Duration. |
|---|---|---|
| Pre-copulation Period . . . . . . | 11–13 | 12 |
| Copulation to Oviposition . . . . . | 3–5 | 4 |
| Oviposition Period . . . . . . | 54–106 | 71 |
| Post-oviposition Period . . . . . | nil | 3 |
| Total Duration of Adult Life * . . . . | 70–126 | 89 |

* After emergence from mine.

* Once a week the palms were removed from the cages and new ones inserted, and twice a day the palms were sprayed with water.

Egg-capacity observations were made concurrently with the observations summarised in the above table. The egg-capacity was found to vary from 91 to 164, for the 9 beetles which appeared to behave normally, the mean being 122. The great variation in the observed egg-capacity and in the duration of the oviposition period (and therefore of the adult life) appeared to be due to variation in size of the beetles, not to the conditions of confinement. The smaller beetles laid fewer eggs and did not live so long. The number of eggs laid per day was, on the average, 1 for the first 2 days, then 2 for 8 days, then 3 for 16 days, then 2 and finally 1 for very variable periods. Every beetle showed a similar increase and decrease in the number of eggs per day, and the maximum number per day was 3 in every case. This, together with the uniformity exhibited in the post-oviposition period, indicates that the data obtained for the duration of the oviposition period and the egg-capacity were normal, in spite of the great variation observed.

Females which were not given an opportunity for pairing began *ovipositing at the usual time but at a subnormal rate*. They laid 1 egg per day for 2 weeks, and all these eggs were infertile. After 2 weeks they were provided with males and pairing invariably occurred immediately; eggs were laid from this time onwards at the rate of 2, and occasionally 3, per day. All the eggs laid after pairing had occurred were fertile, regardless of whether oviposition bad commenced before pairing occurred or not.

The males were never attracted to the females until the latter were at least 9 days old, and no actual pairing ever occurred until they were at least 11 days old. Pairing, having once commenced, occurred nearly every day throughout the oviposition period of every female, but it is probable that the beetles pair abnormally frequently in confinement. Certainly frequent pairing is unnecessary for fertilisation of the eggs. The first pairing usually lasted for about 4 hours and subsequent pairings for much shorter periods.

*The adult life of the male was found to vary in duration from 86 to* 155 days (mean 110 days for 12 beetles). The duration of the pre-copulation period for males was determined by enclosing males, as soon as they emerged, with much older females; this period was found to vary from 14 to 20 days, the mean being 16 days, which is considerably longer than the corresponding period for females.

The sexes occur in approximately equal numbers, but the number of beetles for which sex records were kept was not large enough to serve as a basis for a more accurate estimate.

When the adult life and egg-capacity of *P. nuciferae* are compared with those of *P. reichei*, the following important points are noticed:—

i. The females of *P. nuciferae* do not begin to oviposit so soon as those of *P. reichei*, but the pre-oviposition periods are nevertheless comparable.

ii. The adult life of *P. nuciferae* is very long, and is at least 3 times as long as that of *P. reichei*, on the average.

iii. The egg-capacity of *P. nuciferae* is large, and is at least 6 times as large as that of *P. reichei*, on the average.

iv. The much longer duration of the adult life in *P. nuciferae* is due almost entirely to the oviposition period.

It is reasonable to suppose that some of the differences in habits which we have already noted are associated with these great differences in the oviposition periods and the egg-capacity. Thus, the gregarious habit is unnecessary in *P. nuciferae* since the long adult life in itself provides a sufficient chance of the sexes meeting. Again, the fact that *P. reichei* immediately drops when subjected to any abnormal disturbance and that *P. nuciferae* does not do so, suggests that the habit of dropping is a necessary protection in an insect which is both brilliantly coloured and gregarious, in which case it is partly attributable, through gregariousness, to the short oviposition period.

From the data already given, it is clear that the mean duration of one generation, as estimated in the same manner as for *P. reichei*, is approximately 106 days (3½ months), which is very nearly the same as for the latter insect. The egg-capacity of *P. nuciferae*, however, is very much greater than that of *P. reichei*, and consequently the potential rate of multiplication is very much greater in the case of *P. nuciferae*. Thus, in a period equal to 3 mean generations, a single female of *P. nuciferae* (assuming numerical equality in the sexes) can give rise to approximately 454,000 individuals, as against the 1,760 derived from a single female of *P. reichei* in the same time and the same number of generations.

In spite of this enormous superiority of *P. nuciferae* as regards rate of multiplication, *P. reichei* is a pest and *P. nuciferae*, in Java, is not, which at first suggests that the indigenous natural enemies in Fiji are potentially infinitely less efficient than those in Java. This, however, is an erroneous conclusion. We have, in fact, seen that in the absence of *Pediculoides ventricosus*, which must be regarded as an intruder, the indigenous parasites in Fiji are efficient controlling factors. The true reason for the difference in the economic status of the two species is that whereas *P. reichei* has a very short oviposition period, relative to the period of development from the egg, *P. nuciferae* has an oviposition period which is considerably longer than the period of development. In both cases, the indigenous parasites depend for their efficiency upon the presence of all stages of their respective hosts simultaneously and constantly, and in the case of *P. nuciferae* this condition is inevitable because the long oviposition period ensures that even if the one-stage condition is temporarily established it must give way, in one generation only, to the multiple-stage condition. In *P. reichei*, on the other hand, the one-stage condition, having once been established, cannot be completely lost for at least 3 generations and the parasites are rendered comparatively useless throughout this time in consequence.

## E. Observations on *Gonophora xanthomelana*, Wied.*

(Plate XX.)

*G. xanthomelana* proved of some importance in connection with the campaign against *P. reichei* because it is an alternative host of some of the

* The specimens thus determined were reared by the writer from banana and *Amomum* and were believed by him to be distinct from *G. xanthomelana*, Wied., which was already well known as a pest of orchids. Dr. Spaeth, however, to whom they were submitted by the British Museum, found them to be conspecific with specimens of *G. xanthomelana* from orchids.

parasites of *P. nuciferae*. In West and Central Java, this Hispid, the principal food-plant of which is the cultivated banana, is very generally distributed. Bananas abound in every native village and the insect, or traces of its presence, can usually be found upon the leaves here and there in any locality if a thorough search is made. It is never common, however, and is entirely unknown as a pest of bananas, although it is potentially capable of doing severe damage. It was never found by the writer in the dry eastern end of Java. Its vertical distribution extends from sea-level to about 3,000 ft.

*G. xanthomelana* feeds, not only on the cultivated banana, but also on other species of Musaceae on Orchids, and on *Amomum* (Zingiberaceae) in the mountain forests. These alternative food-plants account for its extensive vertical distribution. It is recognised as a pest of orchids. We are here concerned principally with its activities on bananas.

The eggs are laid, end-to-end, in single rows on the undersides of the leaves of the banana. A row contains from 3 to 6 eggs, each egg being separately inserted into the leaf tissues through a broad slit made in the epidermis by the adult. The eggs themselves are not visible, each one being separately covered, immediately after it is laid, by a small deposit of excrement which projects from the leaf surface and which, together witb the others of the same row, renders the eggs comparatively easy to find.

The larvae mine in the leaves. All the larvae from any one row of eggs feed together in the same mine, usually side-by-side, so that those mines in which all the larvae mature are very large and cause great reduction in the functioning leaf surface. In the great majority of mines, however, several of the larvae are destroyed while young by natural enemies, and not infrequently all of them are destroyed. The mines form conspicuous brown patches upon the leaves, but are nevertheless difficult to find, as a rule, on account of their resemblance, except at close quarters, to the patches of dead tissue which often abound on banana leaves and are due to wind and fungi. There are three larval instars. Pupation takes place within the mine, and the adults escape through slits in the epidermis.

The duration of the life cycle from oviposition to emergence from the mine was found to vary from 56 to 61 days at Buitenzorg in October and November, 1932, and the incubation period at the same time and place proved to be 17 days. The rate of development is therefore nearly the same as that of *P. nuciferae*. In the mountains, however, the development is considerably slower, but no complete records were obtained.

The adults feed singly upon the undersides of the leaves, making incisions very similar to those made by *Promecotheca* spp. in coconut leaves.

### F. The Bionomics of the Parasites of *P. nuciferae*.

#### 1. **Dimmockia javanica**, Ferr. (Eulophidae.)

a. *Description of Stages*. Egg (Plate XII). The egg is very similar to that of *E. hispidarum*, but differs in that it is smaller, narrower relative to its length, and its greatest width is nearer its anterior end. The length varies from 0·33 mm. to 0·36 mm., the mean being 0·34 mm.

1st Instar (Plate XII). The segmentation is very distinct. There

are 13 segments (excluding the head). The larva is broadly rounded anteriorly, the head being large, and posteriorly it tapers to a point. The back is strongly arched, the ventral surface straight. The greatest width is at about the 4th segment when the larva is newly hatched. The mouth-parts are situated on a lobe which projects ventrally from the head. Mid-ventrally, there is a longitudinal row of 7 fleshy intersegmental protuberances, functioning as pseudopodia. There is no pseudopodium between segments 1 and 2, the first being between segments 2 and 3 and the last between 8 and 9. The 13th segment also serves as a pseudopodium. There are no dorsal pseudopodia in this instar (or in any instar except the last). The skin is shiny and very transparent. There is a single row of numerous minute points across the back of each segment, near the posterior border. These points extend down the sides below the spiracles but are not present ventrally. Otherwise the skin is entirely smooth and shiny (cf. *E. hispidarum*). There are invariably only 4 pairs of spiracles, situated slightly dorsally on segments 2, 4, 5, and 6. The 3 thoracic segments bear one pair of minute tubercles each, on their ventral surfaces.

The length of the newly-hatched larva is 0·28 mm., and the width of the head varies from 0·05 to 0·07 mm.

2nd Instar. The skin in the 2nd instar is absolutely smooth and shiny throughout, the raised points of the 1st instar having been entirely lost, and there are no pseudopodia, ventrally or dorsally. There are still only 4 pairs of spiracles, however. The segmentation is very distinct, except at the end of the instar, when the skin is so tightly distended that the segmentation is rendered obscure. The width of the head varies from 0·10 to 0·12 mm.

3rd Instar. This instar is identical with the 2nd in all respects except size and the number of spiracles. The full complement of spiracles is now present, there being 9 pairs in all, situated on segments 2 to 10 inclusive. The width of the head varies from 0·14 to 0·17 mm.

4th (last) Instar. The 4th-instar larva is absolutely identical, except in certain minute details, with that of *E. hispidarum*. The figures of the latter (Plate XIII) apply in every particular to this species also, and no means of distinguishing the 2 species, other than by killing them and subjecting them to minute microscopic examination, could be found.* Except in extreme cases, size is no criterion because both species vary greatly in the size ultimately attained in this instar (though not in earlier ones) according to the number of individuals per host and the size of the host. The description for *E. hispidarum* applies to this species also in every particular except (figs. 9 and 12) :—

i. The shape of the mandibles, which in *D. javanica* have the points slightly more curved, while the shape of the basal structures is different.

ii. The size of the ocelli, relative to the mandibles; in *D. javanica*, the ocelli are appreciably larger.

iii. The chitinisation of the antennae, which, in *D. javanica*, are brown at the tips only.

iv. The cuticular thickenings which support the mouth, which are more extensive in *D. javanica*.

* The necessity for distinguishing the 2 species arose through the introduction of *D. javanica* into Fiji.

A further difference is that in *D. javanica* the basal parts of the mandibles often are not strongly chitinised and are therefore colourless, but this is not constant.

The maximum length attained by larvae of *D. javanica*, when fully

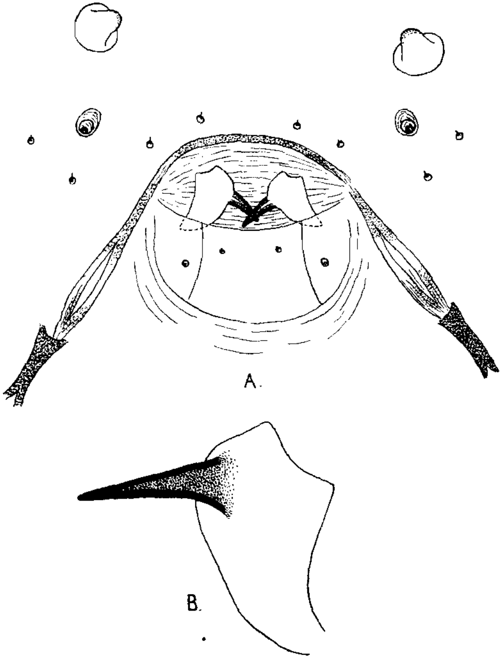



FIG. 12.—*Dimmockia javanica.* A, mouth-parts and associated structures of full-grown larva; B, mandible. (For further explanation, cf. fig. 9.)

extended, is 3·13 mm.; this is less than the maximum for *E. hispidarum*, but since few individuals attain the maximum size, measurement seldom serves for specific determination.

Prepupa (Plate XIII). The prepupa is white, translucent, and shiny. It is readily distinguishable by its shape from that of *E. hispidarum.*

The body, excepting the posterior third, is nearly cylindrical. The first segment is very large. The abdominal segments are wrinkled transversely.

Pupa (Plates XIV and XV). The pupa is translucent and brownish-yellow in colour. (It becomes black and opaque shortly before the contained adult emerges.) The surface is shiny. There is a large blotch of a rich dark brown colour in the centre of the thorax dorsally and another of the same colour on the abdomen, but these vary greatly in intensity, sometimes being nearly absent and sometimes nearly black. The most noteworthy features, apart from the general shape and colour, are the pointed projection at A and the deep indentation at B (Plate XV). None of the appendage sheaths extends as far as the extremity of the abdomen. The pupa varies greatly in size, the length of the largest being 2·5 mm. and of the smallest 1·4 mm.

The male pupa is slimmer than the female, and males are always smaller than females of the same batch.

Adult. The adult is described by Ferrière in *Stylops*, **2**: 92, 1933. The sexual dimorphism is very marked, the male being recognisable at a glance by its three-branched antennae and the transparent anterior third of the abdomen.

b. *Life History*. *D. javanica* is an external primary parasite of the larva of *P. nuciferae*, attacking all the larval instars. It was introduced into Fiji and attacked *P. reichei* as readily as it attacks its normal host in Java. It appears to frequent coconuts only, differing in this respect from all the other parasites of *P. nuciferae*. It is abundant in all parts of Java, wherever its host occurs.

The habits of *D. javanica* are identical in almost every detail with those of *E. hispidarum*, already described. The only important difference is that the former does not begin to attack the host mines until towards the end of the 1st instar, while the latter attacks all 1st-instar mines equally readily, regardless of age. This difference is as evident in the laboratory as in the field. In glass tubes, females of *D. javanica* can very seldom be induced to attack mines which are less than 1·5 cm. long, but the same females immediately attack mines which are 2 cm. or more in length. *E. hispidarum*, on the other hand, shows no reluctance to attack the younger mines.

*D. javanica* lives and breeds very satisfactorily in captivity, when kept in glass tubes and fed regularly with honey. Studies of the duration of the adult life, the egg-capacity, and the rate of oviposition, were therefore comparatively simple and yielded reliable results. Two identical experiments were conducted for this purpose, one in Java and one in Fiji. On each occasion 40 females and 40 males, all of which emerged on the same day, were used. They were placed in pairs in separate glass tubes, and each pair was provided every day with a fresh, 3rd-instar, mine. The mines removed each day were all opened and thoroughly examined under a microscope, the number of eggs in each being counted and recorded. Every female was dissected when it died, and the eggs, if any, which still remained in the ovaries were counted. In this way, a separate egg record was obtained for every female.

It was found that the mean duration of life for females which are constantly provided with mines for ovipositing is 31 days, varying from

24 days to 50 days. The mean duration of life for males proved to be nearly the same as for females, but the maximum was 44 days. Every female had a preoviposition period of at least 3 days, but in a few cases this was considerably longer, the maximum being 9 days. There was invariably a short post-oviposition period also, and this varied in duration from 2 to 4 days. Neither the duration of the oviposition period nor that of the adult life was found to have any connection with the egg-capacity. The individual which produced the greatest number of eggs lived only 29 days, and several individuals which lived longer than 40 days produced only the average number of eggs. The size of the individual proved to be the factor determining the egg-capacity. Dissections showed that although the typical number of ovarioles is 3 per ovary or 6 per female, small individuals invariably have greatly suppressed ovaries, the suppression consisting of reduction in the number of ovarioles, not in uniform reduction in size of the usual 6. Small females usually have both ovaries present, but one ovary usually consists of 2 ovarioles and the other of 1 only. The size of the egg is nearly constant, regardless of the size of the female, and the maximum number of fully-developed eggs which one ovariole can contain at one time is 3. In small females, therefore, the rate of production of eggs is very much less than in large females; and since the duration of life is the same, the egg-capacity varies directly with the size. The females used in the experiments were arbitrarily divided into 3 classes, small, medium, and large, and it was found that the egg-capacity for these 3 classes was approximately 24–30, 30–40, and 40–56 respectively. Large females all laid more than 40 eggs, and 56 was the maximum. The mean egg-capacity for the species (*i.e.* for the 80 females for which records were obtained) was 32·7. The average number of eggs laid per day by the average female during the whole of the oviposition period proved, when suitable mines were constantly present, to be 1·4. In no instance, however, did oviposition take place every day during the oviposition period. Nearly all individuals began by laying a few eggs every day for several days, then ceased ovipositing completely for a few days (2 to 8), then again laid every day for several days, and so on. Except that oviposition took place in this same general way in nearly all cases, no uniformity was apparent. Nearly all the females proved, on dissection at death, to have laid all their eggs, their ovaries being completely devoid of eggs in any stage of development. Some of them, however, died with a few eggs unlaid, but never more than 4. In these latter cases, the eggs in the ovaries at death were included in the egg-capacity estimates, which are detailed above.

Separate experiments were made to ascertain the maximum number of eggs which could be laid in one day. The females used for these experiments were all large, and were given no opportunity to oviposit until they were 2 weeks old. They were then provided with two 3rd-instar mines each. It was found that none of them laid less than 10 eggs in the day, that the majority laid either 17 or 18, and that 18 was the maximum. On the following day, more mines were provided, but none of the females (with one exception) laid any eggs. Thus, the maximum number of eggs which can mature at one time is 18, *i.e.* 3 in each ovariole. The same figure was obtained for *E. hispidarum*, the ovaries of which are almost identical.

The sex ratio could not be determined in the field in Java because, as in the case of *E. hispidarum*, it varies according to the stage of the host attacked. In individuals from 1st-instar mines, the sexes are approximately equal numerically, but in large mines the males are always a minority. Collection of mines in the field always results in an unnatural preponderance of large mines, these being much more readily seen, and consequently any estimate of the sex ratio on such a basis is inaccurate. The sex ratio for individuals resulting from eggs laid in 3rd-instar mines by paired females was, however, determined in Fiji in the course of bulk-breeding work in the laboratory. In these circumstances, it was found that females were more numerous than males in the proportion of 3 : 2 (2,414 ♀♀ and 1,594 ♂♂).

The host ceases to be liable to the attack of *D. javanica* as soon as the skin hardens after pupation. Mines containing prepupae are subject to attack, and if the attack of the parasite is made 2 days or less before the end of the prepupal period, pupation is not prevented. Since the stinging of the larva always stops development, it is remarkable that the stinging of the prepupa does not prevent pupation. The parasite larvae can feed and mature provided they begin feeding before the pupal skin hardens. This means that if the larvae are to develop the host must be attacked by the parent parasite about 2 days before the pupation of the host is normally due (2 days being the incubation period of *D. javanica*, approximately). If the initial attack by the parasite occurs any later than this, the parasite larvae cannot begin feeding because the pupal skin is too hard, and they die of starvation. In the field, it is extremely unusual to find *D. javanica* larvae feeding upon pupal hosts, and only 2 such instances are known. *D. javanica* is never attracted by mines containing pupae and is a true larval parasite.

c. *Life Cycle.* The life cycle at a daily mean temperature of 84° F. (absolute maximum 89° F., absolute minimum 77° F.) is as follows :—

| | | |
|---|---|---|
| Incubation Period . . . . . . . . . | | $1\frac{3}{4}$ days |
| 1st Instar ,, | $\frac{3}{4}$ day | |
| 2nd ,, ,, | $\frac{3}{8}$ ,, | |
| 3rd ,, ,, | $\frac{1}{2}$ ,, | |
| 4th ,, ,, | $3\frac{1}{4}$ days | |
| Prepupal Period | $\frac{5}{8}$ day | |
| Total Larval Period . . . . . . . . | | $5\frac{1}{2}$ ,, |
| Pupal Period . . . . . . . . . | | $7\frac{1}{2}$ ,, |
| Total Period (to emergence from pupa, not from mine) . | | 15 ,, |

These figures, which agree remarkably closely with those obtained for *E. hispidarum* at the same temperature, are means for 20 individuals, correct to the nearest $\frac{1}{8}$ day. The figures for the total larval period and the total period were obtained, not by adding the component figures, but by independent observation. The 4th instar, as estimated above, includes the period between the cessation of feeding and excretion, which is $1\frac{3}{4}$ days, the 4th-instar feeding-period covering $1\frac{1}{2}$ days. Excretion marks the commencement of the prepupal period.

A proportional lengthening of each stage takes place as the temperature falls. In the cool season in Fiji, at a daily mean temperature of 77° F. (absolute maximum 84° F., absolute minimum 70° F.) in the room in which the experiments were conducted, the total period covered 17 days.

2. **Pleurotropis painei**, Ferr. (EULOPHIDAE.)

*P. painei* is an internal primary pupal parasite. It parasitises *P. nuciferae*, *G. xanthomelana*, *G. taylori*, and bamboo Hispids. It is never secondary. It is very rare as a parasite of *P. nuciferae*, but very common as a parasite of *G. xanthomelana*, and is often common in mines of the latter in bauana leaves aud entirely absent in mines of *P. nuciferae* in coconuts directly above the bananas. It is present in the mountain forests as well as in the plains, and has a considerable variety of hosts, but it was never obtained from Hispids mining in grasses, and there are evidently certain plants, including grasses and coconuts, that it seldom visits.

The host iudividuals are liable to be attacked by this parasite immediately they pupate, and the attack invariably results in the death of the victim a few hours later. The adult parasites take very little notice of a mine containing a prepupa, but immediately pupation takes place they crowd on to the mine and begin ovipositing. In certain artificial conditions, however, the parasites can occasionally be induced to attack prepupae; the resulting progeny develop normally until they are about half-grown, and a few sometimes become full grown, but all invariably fail to pupate and die as larvae, the majority dying long before they are full grown. It is evident, therefore, not only that *P. painei* normally attacks pupae only, but also that it is unable to mature in any other stage of the host. Pupae of any age are attacked, and even those in which the adult beetles are fully developed and about to emerge are not immune. Experiments showed, however, that unless the host pupa is attacked 2 days or more before the adult is mature and due to emerge from it, the parasites within it cannot mature and die without pupating. Thus, in the case of *P. nuciferae*, whose pupal period is 11–12 days, the critical age of the host as far as *P. painei* is concerned is 9 days, and it was found that in pupae 9 days old the parasites sometimes mature and sometimes die prematurely, as larvae.

*P. painei* lays many eggs in each host individual, and it was found that unless the number of eggs exceeds 3, the resulting larvae die when full grown because they cannot completely devour the contents of the host body and are prevented, by the liquid which remains, from breathing through their spiracles at the time when they would normally begin to do so. The number of eggs normally laid, in natural conditions, in one individual of *P. nuciferae* or *G. xanthomelana* varies from 6 to 15, and is usually about 13, but in laboratory conditions more than 15 eggs are commonly laid, and as many as 25 parasites can mature in a single pupa of either of these two Hispids. The adult parasite, when ovipositing, takes up a position on the underside of the mine and inserts its eggs directly into the host pupa, penetrating the wall of the mine and the pupal skin in one operation. Each egg is laid separately, the ovipositor being withdrawn, after each egg is laid, and reinserted in a different position. All parts of the host are attacked equally. The parasite, after having laid a

few eggs from the lower side of the leaf, often moves round to the upper side and lays more there. The eggs are not attached in any way, but are merely deposited in the body fluid.

The effect upon the host is immediate, but it does not immediately die. It becomes lethargic as soon as it is stung, and apparently does not feel any of the insertions of the ovipositor after the first. If, however, it is removed from the mine and touched heavily it proves still to be capable of energetic wriggling. But the lethargy increases and death follows after about 24 hours, there being no long period of paralysis and no further development. At the points in the pupal integument at which the ovipositor of the parasite entered, minute dots appear in about 12 hours, and it is possible to ascertain, approximately, the number of eggs laid from the number of puncture dots visible on the surface.

The eggs are extremely similar in every respect to those of *P. parvulus*. The shape is, however, slightly different, the egg of *P. painei*, when viewed dorso-ventrally, having straighter sides (cf. figs. 13 and 15).

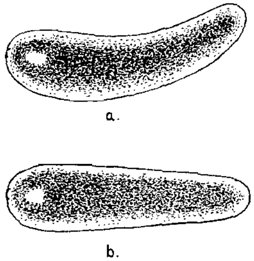



FIG. 13.—*Pleurotropis painei*; egg. a, right lateral; b, dorsal.

The death of the host occurs before the eggs of the parasite hatch. The parasite larvae grow rapidly, feeding in all parts of the bost body, and are readily visible through the host skin 3 days after hatching. They eventually consume the body contents of the host completely, leaving only the integument, which subsequently dries and becomes hard, brittle, and dark brown in colour. Excretion and pupation invariably take place within the host skin, and each individual, as a pupa, is attached to its own excrement, which soon becomes very hard, by its larval skin.

The full-grown larva is indistinguishable from that of *P. parvulus*. Even the mandibles are identical in the 2 species. The pupae are very similar, but are nevertheless distinguisbable. That of *P. painei* is black and shiny, with a slight brown gloss (never blueish or purple), and the shape of the ventral thoracic plate (fig. 17) is characteristic and serves as a means of determining the species from empty pupal skins as well as from pupae.

The adult parasites remain within the host for about 24 hours after emerging from the pupae, and then escape by biting a ragged hole in the

posterior abdominal segment of the host integument, usually dorsally, but sometimes ventrally. All of them emerge through the one hole, except in special circumstances. This position of the exit hole is highly characteristic. The only circumstances in which the hole is made in any other part of the host body, or in which the parasites make more than one hole, are when they are prevented from reaching the posterior extremity of the host by the presence of secondary parasites or dead individuals of their own species. The parasites escape from the mine by biting a circular hole in the upper wall.

The adult life of both sexes is long. The majority of females lived more than 40 days, many lived more than 50 days, and 1 lived 79 days. Males lived more than 30 days as a rule, but seldom more than 40. Pairing occurs as the parasites emerge from the mine, the males waiting at the emergence hole for the females. Parthenogenesis can occur and produces males only, but it was never known to occur in the field. There is always a great predominance of females, but almost every batch includes at least one male. The sex ratio for individuals obtained from *P. nuciferae* and *G. xanthomelana* collected in the field was ♀ : ♂ = 3·7 : 1·0 (156 ♀♀ and 42 ♂♂). Both sexes are strongly heliotropic.

The life cycle, determined at Buitenzorg, Java, is as follows :—

| | |
|---|---|
| Incubation Period . . . . . . . . . | 2½ days. |
| Larval ,, . . . . . . . . . | 8 ,, |
| Pupal ,, . . . . . . . . . | 12 ,, |
| Total Period (to emergence from pupa) . . . . . | 22½ ,, |

These figures are means, based on 51 parasitised pupae of *P. nuciferae* and *G. xanthomelana*, in 30 of which the parasites were reared right through from eggs to adults, while the other 21 were dissected to ascertain the incubation period. The incubation and pupal periods were found to be constant, and the variation in the larval period was not great (7 to 9½ days). The duration of the total period (oviposition to emergence) varied from 20 to 24 days.

The adult is described by Ferrière in *Stylops*, **2** : 94, 1933.

3. **Pleurotropis parvulus,** Ferr.

*P. parvulus* is the parasite which was successfully used eventually as a control for *P. reichei* in Fiji. On account of its importance in this respect, a detailed account of it is given separately in Section VII, and it is only necessary here to refer to its general habits and the respects in which its habits differ from those of the closely allied *P. painei*.

*P. parvulus* is a primary internal parasite of the larva and the pupa of *P. nuciferae*, and also of *G. xanthomelana*, attacking both equally commonly; and it attacks all the larval instars, as well as the pupa, equally readily. It suits the number of eggs laid to the size of the host, but as a pupal parasite it lays rather more eggs in each host individual than *P. painei*. The attack of the adult *P. parvulus* has no effect upon the host, which continues to develop normally for a considerable period before it is finally killed by the parasites within it, and this is the principal bionomic

difference between *P. parvulus* and *P. painei*. *P. parvulus* usually makes more than one emergence hole in the host, and very rarely makes a hole at the posterior extremity of a host pupa, differing in both of these respects from *P. painei*. The females of *P. parvulus* are strongly heliotropic, but the males are not. The rate of development of *P. parvulus* varies greatly with the size of the host; that of *P. painei* is nearly constant, since this species attacks the pupa only, and the size of the pupa is nearly constant.

4. **Achrysocharis promecothecae,** Ferr. (EULOPHIDAE.)

*A. promecothecae* is an egg parasite. It parasitises eggs of Hispids in coconut, banana, Zingiberaceae, bamboo, grasses, and probably other plants. It appears to be most abundant as a parasite of *G. xanthomelana*, but is nevertheless common as a parasite of *P. nuciferae*. It was found throughout Java, in the mountains as well as in the plains, and it is the only parasite known to attack eggs of *P. nuciferae*.

*A. promecothecae* is not a typical egg parasite, however. It attacks only those eggs in which the development of the embryo is already far advanced, and it attacks eggs which are about to hatch more readily than any others. In the laboratory at Buitenzorg it was induced, with difficulty, to parasitise recently laid eggs, but the resulting larvae almost invariably died either when they were full grown or earlier. Eggs of *P. nuciferae* appeared first to become attractive to this parasite when they were about 10 days old. The attack of the adult parasite does not prevent further development of the host embryo, but the latter is killed by the parasite larva within it about 5 days later. Eggs of *P. nuciferae* which are attacked when they are about 10 days old are prevented from hatching, but eggs which are considerably older when attacked hatch normally, the resulting larvae dying soon afterwards. *A. promecothecae*, therefore, is to be found both as an egg parasite and as a parasite of the very young larva, but the adult parasite attacks eggs only.

The female oviposits through the capsule of the host egg, and almost always lays only one egg in each host individual. Very rarely, however, 2 eggs are laid, and it is possible for 2 parasites to mature in one host egg. The parasite larva, when full grown, emerges from the host embryo to pnpate, and pupation takes place in the host egg or, if the latter has already hatched, inside the mine. When the larva, on escaping from the host skin, finds itself in a mine, the excrement is deposited in several separate masses, the larva changing its position slightly dnring the process; and this peculiarity serves to distinguish this species from all other parasites which are to be found in the mines, since all others invariably deposit their excrement in a single mass. The pupa of *A. promecothecae* is black and shiny, and has an indigo sheen. The adult parasite emerges by biting a round hole in the upper epidermis of the leaf, whether it is emerging from an egg or from a mine. The fact that it never escapes through the egg-capsule, as *O. utilis* invariably does when parasitising eggs of *P. reichei*, is no doubt attributable to the manner in which *P. nuciferae* lays its eggs; for the eggs of *P. nuciferae* are sunk into the leaf so that a parasite has only to bite through the thin upper

epidermis to escape, whereas *P. reichei* oviposits on the surface of the leaf and a parasite. if it attempts to escape through the leaf, must bite through all the tissue layers before it can do so.

Pairing takes place on the day of emergence from the host egg or mine, or at any subsequent time. Parthenogenesis can occur, and produces males only, but it appears never to occur in nature. Females greatly outnumber males. 210 individuals were reared in October, 1932, from eggs of *G. xanthomelana* and bamboo Hispids and from mines of *P. nuciferae*, and of these 185 were females, the sex ratio being ♀ : ♂ = 7·4 : 1·0. The simplest method of collecting this parasite in the field is to place a seedling coconut palm or banana plant, bearing many Hispid eggs, under banana plants in which *G. xanthomelana* is present, the leaf-stems of the seedling having first been made ant-proof. If the palm is left for a week, more than 50% of the eggs usually prove to be parasitised, and provided that the adult Hispids are available to lay the eggs in the first place, this method is much less laborious than hunting for eggs laid in natural circumstances in the field.

The incubation period was not ascertained with accuracy, but is between 1 and 2 days, and the mean larval and pupal periods are approximately 10 and 12 days respectively. Excretion takes place about 1 day before pupation. The duration of the total life cycle, from oviposition to emergence from the host egg, varies from 22 to 28 days. The adult parasites (both sexes) lived from 3 to 4 weeks in glass tubes.

The development and habits of *A. promecothecae* are of special interest when compared with those of a typical egg parasite, such as *O. utilis*. *A. promecothecae*, as we have seen, is more a larval parasite than an egg parasite, although the host is attacked before leaving the egg; and it develops like a typical larval parasite in that it proceeds to excrete and pupate as soon as it is full grown. *O. utilis*, on the other hand, attains its maximum growth with extraordinary rapidity and then undergoes an extremely long resting period before excreting or pupating. Both are egg parasites, but the one is primarily adapted to develop in the advanced host embryo and the other to develop in the less differentiated and more liquid contents of the egg during the earlier stages of incubation.

The adult of *A. promecothecae* was described by Ferrière in *Bull. ent. Res.* **22**: 289, 1931.

### 5. **Polysphincta** sp., **Opius** sp., and **Cirrospilus** sp.

Extremely little is known concerning the habits of these 3 species, as they were obtained so rarely that a study of their habits was impossible. Concerted efforts were made to obtain them in the field from several different hosts, but all efforts failed, and they were only obtained in the course of more general field work when they were least expected.

*Polysphincta* sp. attacks larvae of *P. nuciferae* and bamboo Hispids. It constructs a long, white, silken cocoon in the mine, outside the host. 2nd and 3rd-instar larvae of *P. nuciferae* are attacked. In 2nd-instar mines, there is only one individual of the parasite per mine; but in larger mines there may be two, in separate cocoons. Judging from the appearance of the remains of the host larva, this is an external parasite, but no

definite proof of this was obtained. The adult emerges by biting a large ragged hole in the mine. The adult life is probably long, a female having survived for 6 weeks. All attempts to induce this species to oviposit failed. It would frequently pierce a mine, though not the larva, with its ovipositor, but no eggs were ever laid, and subsequently it would invariably bite a hole in the mine and devour the larva.

*Opius* sp. is also a primary larval parasite, attacking bamboo Hispids and *P. nuciferae.* It was found on only 3 occasions. On each occasion there was only one individual in the mine, and this was a pupa in a brown, ribbed, cocoon. A female lived 59 days.

The third species, *Cirrospilus* sp., was obtained, almost certainly as a primary parasite, from larval mines of *P. nuciferae, Aphanisticus latus,* and bamboo Hispids. It is probably an external parasite, but this is not certain. There are several individuals per mine (2 to 7) and the pupae, which are black and shiny, are attached to the excrement, and therefore to the mine, by the larval skins. All the females obtained lived longer than 6 weeks, and one lived 73 days.

6. **Pleurotropis detrimentosus,** Gahan. (Eulophidae.)

*P. detrimentosus* is a secondary parasite. Its normal hosts are *D. javanica, P. painei,* and *P. parvulus,* and it attacks all of these very commonly. It frequents coconuts and bananas equally, and is commonly obtained, therefore, from the mines of both *G. xanthomelana* and *P. nuciferae,* but it is never obtained from mines in bamboo. It occasionally attacks *Achrysocharella orientalis* in mines of *P. nuciferae,* and is then a tertiary parasite.

*P. detrimentosus* plays exactly the same rôle in Java as *T. taylori* in Fiji, and the habits of these 2 parasites are almost identical. *P. detrimentosus* oviposits, from the undersides of the leaf, in large larvae and prepupae of any of the above-named parasites, but it does not oviposit in pupae. It lays only one egg in each host individual. The host is not immediately affected, but continues to develop normally for a few days. If the host, when attacked, is a feeding larva, or a larva which has only just completed feeding, it is killed by the contained parasite as a prepupa; if, on the other hand, the host is a prepupa when attacked, pupation takes place before death occurs. The larva of *P. detrimentosus,* when full grown, almost entirely fills the host skin. If the host dies as a prepupa the parasite nearly always emerges from the host skin to pupate, and in this case the host skin, being extremely fragile and usually completely emptied, often cannot be detached afterwards, so that there is, at this and later stages, nothing to show that *P. detrimentosus* was not a primary. If the host dies as a pupa, *P. detrimentosus* often pupates inside the host skin, but equally often it pupates outside, the host pupal skin remaining clearly apparent as evidence of the true status of *P. detrimentosus.* Thus, the pupa of *P. detrimentosus,* according to the species and the stage of the host, may be found unprotected in the mine, or enclosed within a pupal skin of *D. javanica,* or inside a Hispid larval or pupal skin but otherwise not enclosed, or enclosed within a pupal skin of *P. painei* or *P. parvulus* inside a Hispid skin. When the host is *D. javanica* and the parasite larva

emerges from it to pupate in the mine, the excrement is deposited against the wall of the mine in a single mass and the old larval skin persists as a means of attachment of the pupa, in exactly the same way as in *D. javanica*. The pupa of *P. detrimentosus*, however, is at once distinguishable from that of *D. javanica*, being black, shiny, and opaque. The shape of the pupa and the outline of its ventral thoracic plate (fig. 17, p. 184) serve to distinguish it from *P. painei* and *P. parvulus*, with either of which it is often to be found in the same *Promecotheca* skin.

The habits and appearance of the full-grown larva of *P. detrimentosus* are entirely different from those of the other secondary parasite, *A. orientalis*. The larva of the latter species, when full grown, is very active and its skin is rough. *P. detrimentosus* is extremely lethargic and slow in its movements, and its skin is smooth and very shiny; it is, in fact, of the typical Chalcid form, and extremely similar in appearance and behaviour to the larvae of *P. painei* and *P. parvulus*.

*P. detrimentosus* sometimes parasitises all the individuals of *D. javanica* or one of the internal primaries which are present in a mine. Far more frequently, however, it parasitises only a few of them, so that individuals of both primary and secondary parasites emerge from the same mine. In this connection it is interesting to note that 3 species of parasites not infrequently emerge from one mine. The Hispid individual is first attacked by one of the internal primaries or by *D. javanica*, and then *P. detrimentosus* and *A. orientalis* attack different individuals of the primary parasite; or alternatively, *P. detrimentosus*, as a tertiary parasite, attacks some of the individuals of *A. orientalis*, which have parasitised one of the primaries.

The duration of the total life cycle of *P. detrimentosus*, from oviposition to emergence from the pupa, varies from 14 to 16 days. Emergence from the mine takes place a day after emergence from the pupa. The period covered by the life cycle is such that *P. detrimentosus*, although secondary, very often emerges from the mine at precisely the same time as individuals of *P. painei* or *P. parvulus* from the same mine, though it cannot emerge at the same time as *D. javanica*. The maximum record for the length of the adult life of the female was 60 days.

Males are rather more numerous than females, and in this respect *P. detrimentosus* differs from all the other parasites investigated in Java.

### 7. **Achrysocharella orientalis**, Ferr. (EULOPHIDAE.)

a. *Hosts*. *A. orientalis* is a secondary parasite only. It attacks *D. javanica*, *P. painei*, and *P. parvulus*, and it frequents coconuts and bananas equally. It was never obtained from mines in bamboo or rice, or from any mines other than those of *P. nuciferae* in coconuts. It is the most important natural enemy of *P. parvulus*, and a detailed study of its habits was found necessary before a proper understanding of the potential economic value of the latter could be gained. It does not attack the parasites of those Hispids (*Bronthispa* and *Plesispa* spp.) which are common in coconut palms but are not miners.

b. *Distribution*. This secondary parasite was found in all localities, throughout Java, in which *P. nuciferae* or *G. xanthomelana* were present, and its vertical distribution extends from sea-level to about 3,000 ft.

c. *Life History*. *A. orientalis* is an internal parasite. The egg is laid inside a full-grown larva, prepupa, or pupa of any of the hosts named above, but earlier stages are not attacked. The stage of the Hispid host of the primary parasites is immaterial. The egg is deposited in the body cavity of the host and is unattached. Normally there is only one egg per host, but when the host is a *Pleurotropis*, two or more eggs may be laid, accidentally, in one individual on account of the crowding together of a large number of *Pleurotropis* individuals inside the Hispid skin and the consequent inability of the secondary parasite to discriminate between them from outside the mine. Only one individual develops in each host, however. *A. orientalis* occasionally oviposits in all the primary individuals present in one mine, but more usually it attacks only 50% or less. Its habits, however, are such that even if only a small percentage are initially attacked all the individuals present are often killed ultimately. The attack of *A. orientalis* has no immediate effect upon the host. The host, if attacked as a larva, excretes normally but dies as a prepupa; and if it is

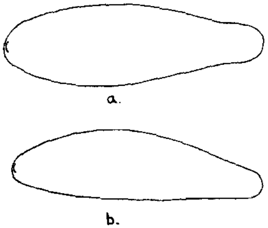


FIG. 14.—*Achrysocharella orientalis*; outline of egg. a, dorsal; b, left lateral.

attacked as a prepupa, the host pupates normally and dies as a pupa. In either case, death is directly due to the contained parasite, not to the initial attack of the parent parasite.

In very many instances, the true status of *A. orientalis* within the mine is obscure, unless its habits are thoroughly understood. As a parasite of *D. javanica*, the external primary, it sometimes causes all trace of the primary individuals in the mine to disappear completely and pupates unprotected in the mine, just as *D. javanica* itself does. The mine otherwise contains only the remains of the Hispid, which has obviously been attacked externally, and there is nothing to indicate that *A. orientalis* was not an external primary, although actually it was an internal secondary. Equally frequently, when it attacks one of the internal primaries, it leaves no traces whatever of the latter and appears to be an internal primary itself. Of many experiments which proved its true status, the most conclusive was one in which 80 females, all eager to oviposit, were put in 40 tubes (2 per tube) and were provided with large mines of *P. nuciferae* (1 per tube) in which to oviposit. Of these mines, 20 contained healthy larvae while the other 20 contained larvae parasitised by *P. parvulus*, the

individuals of which had already reached the prepupal stage. After 2 days, the mines were all removed from the tubes and the 20 feeding larvae were inserted into new leaves. The result was that 19 of the 20 larvae attacked by *P. parvulus* eventually yielded *A. orientalis* (one only having yielded *P. parvulus*), and the other 20 all remained healthy and eventually yielded adult beetles.

The habits of the larva are remarkable in that, when the host is *P. painei* or *P. parvulus*, the larva is first a typical internal parasite and then becomes an external predator within the Hispid skin. When the host is *D. javanica*, however, no external predatory period occurs.

The larvae of *A. orientalis*, as parasites of *P. painei* or *P. parvulus*, feed as true internal parasites until they are nearly full grown, and each of them devours every particle of the contents of its host skin. The host skin, if larval, is absolutely transparent and extremely thin, and it fits round the body of the *A. orientalis* larva so closely as to appear at first sight to belong to it. When this stage is reached, the host skin is ruptured and the parasite larva emerges from it. On account of its extreme flimsiness the host skin is often invisible after it is shed. It crumples and shrivels to such an extent that it is indistinguishable among the debris which the Hispid carcase contains. If, on the other hand, the host is a pupa, the empty black skin remains conspicuous, being strongly chitinised; and very often it is ruptured as though an adult parasite of its own species had emerged normally from it.

When inside its host, the larva of *A. orientalis* is extremely sluggish in its movements, and it is quite helpless if it is removed from the host prematurely. As soon as it emerges, however, it exhibits great activity and behaves entirely differently. The change is effected by a moult which is accompanied by anatomical changes. The moult takes place inside the host skin, and the larva emerges from the latter an hour or so afterwards. The larva is now in its last instar. It can crawl rapidly on any surface, inclnding glass, if it is removed from the Hispid skin; but unless the Hispid skin is artificially split, all the larvae of *A. orientalis* remain inside. Pressure on the outside of the Hispid skin causes great activity among the contained hyperparasites. They wriggle with great energy, and can move rapidly from one end of the Hispid skin to the other, pushing their way between those of their fellows which have been less disturbed, and jostling any prepupae or pupae of the primary parasite in all directions if, as is usually the case, a few of these are still present because the female *A. orientalis* which attacked the mine failed to find all of them. All the *A. orientalis* individuals in one Hispid skin emerge from their hosts at approximately the same time, within 12 hours. There is consequently a very sudden change in the appearance of the contents of the Hispid skin as seen by transmitted light through the skin, which is usually sufficiently translucent to enable one to see the contained parasites. For several days, only the motionless pupae or prepupae of the primary parasite can be seen. There is nothing to indicate that the secondaries are present until one day it is observed that most or all of the primaries have disappeared and been replaced by very active secondary larvae almost as large as the original primaries.

As soon as the larvae emerge from their hosts they become ferocious

predators within the Hispid skin. If some of the primary prepupae or pupae remain unattacked these are rapidly devoured; if none, or too few, remain unattacked the secondaries attack and devour one another until those which are victorious are full grown. Frequently, *A. orientalis* oviposits in only a few of the primaries present, and in such cases, the secondaries, on emerging from their hosts, find more than sufficient food available and become full grown without destroying all the primaries. When this occurs the remaining primaries produce normal adults in due course, and these emerge a few days before the secondaries.

The sudden change to the external predatory condition necessitates considerable anatomical changes. In the penultimate instar, which culminates in emergence from the host skin, the larva is incapable of any active movement. It is relatively broad and nearly cylindrical, and its skin is very smooth, shiny, and transparent. The segmentation is indistinct, but with difficulty, 13 segments, in addition to the head, can be distinguished. There are no pseudopodia. The tracheal system is well developed but usually incomplete. A few extremely minute lateral setae are present. In the final instar, the larva is entirely different. It is now greatly flattened dorso-ventrally, the ventral surface being nearly flat and the dorsal only slightly convex. The head is very large and the segmentation is very clearly marked. The 1st segment is by far the largest, the 2nd is shorter, and the 3rd is shorter still, but these segments are all longer than any of the others, which are nearly equal in length. Dorsally, there is a median row of 10 large, intersegmental, protuberances, functioning as pseudopodia, the first between segments 1 and 2 and the last between 10 and 11. There are 8 pairs of spiracles, situated on segment 2 and on segments 4 to 10 inclusive. The skin is covered, dorsally and ventrally, with innumerable minute papillae which give it a rough and very characteristic appearance and render it less transparent than that of earlier instars or of typical internal parasites. It is this roughness which is principally responsible for the great change in appearance which takes place at the last moult. The skin on each of the pseudopodia, however, is devoid of papillae, entirely smooth, and slightly sticky. The pseudopodia are the principal organs of locomotion, and the larva, when crawling, always lies on its back, but locomotion is further facilitated by the roughness of the skin and the presence of minute, stiff, lateral setae (one pair on each of the segments from 1 to 11 inclusive). The mouth opens somewhat ventrally, and just below it is a pair of rounded papillae. The mandibles are strongly chitinised and relatively large, but are not of specially characteristic shape, being simply curved hooks.

As a parasite of *D. javanica*, *A. orientalis* necessarily has different habits in some respects, since the host in this case, although inside the mine, is external to the Hispid, and is, moreover, much larger. A single individual of *D. javanica* is large enough to provide all the food required by the secondary parasite inside it, and in this case the secondary larva is an internal parasite in the last instar as well as in the earlier ones, there being no predatory period.

When the host is *P. painei* or *P. parvulus*, the larva of *A. orientalis* attains a size considerably greater than that of its host, on account of its

habit of continuing to feed after emptying the host skin. As a parasite of *D. javanica*, however, the larva can never become so large as its host.

Excretion and pupation take place inside the Hispid skin when the host is one of the internal primaries. The excrement is deposited in a single mass, and the pupa is attached to it by the last larval skin which takes the form of a minute, slightly twisted, white tape, attached at one end to the posterior extremity of the pupa and at the other to the heap of excrement. The roughness of the larval skin is still distinguishable. When the host is a larva or prepupa of *D. javanica*, the *A. orientalis* larva always emerges from it, to excrete and pupate unprotected in the mine. The host skin shrivels to such an extent that it is most difficult to detect. The larva moves actively over the inside of the mine in search of a suitable site for pupating, and after a few hours it settles down and does not move again. The excrement is deposited against the wall of the mine, and the pupa is attached to it by the larval skin. When the host is a pupa of *D. javanica*, the parasite occasionally emerges from it to pupate, but more frequently it excretes and pupates inside the host pupal skin, having first split it open anteriorly.

The pupa is black and shiny. It is readily distinguishable by its shape from all other species which are to be found in the mines. The outline of the ventral thoracic plate (fig. 18) is characteristic also.

The adult parasites * emerge from the mine by biting one or more neat, circular, holes in the upper epidermis. In those cases in which the parasites, on emerging from the pupae, find themselves inside a Hispid skin, they first escape from the latter by biting one or more holes in any part of it, and these holes are very ragged in outline. Pairing occurs on emergence from the mine. The sexes are very readily distinguishable, the abdomen of the male being white anteriorly, while the female is black throughout. Females are always more numerous than males, the ratio being ♀ : ♂ = 2 : 1. As in the case of the primary parasites, the female is unable to recognise potential host individuals if these are removed from the mines in which they normally lie. It is the mine which provides the initial incentive for oviposition. After investigating the mine from the outside, however, the parasite is able to recognise whether the contained Hispid individual is parasitised or not. If it is parasitised, the female proceeds to oviposit; if not, it wanders off in search of other mines. *A. orientalis* will not oviposit in a parasitised Hispid until such time as the contained parasites have almost completely devoured the contents of their host and air spaces begin to appear inside the host skin. In the case of *P. parvulus*, this stage is reached very soon after the Hispid dies. When a mine containing a living Hispid parasitised by *P. parvulus* is left continuously in a tube with several females of *A. orientalis*, slight interest is shown by one or two of the females from time to time while the Hispid is alive, and occasionally a female thrusts its ovipositor through the mine as if about to oviposit, but no eggs are ever laid and the attempt is soon abandoned. This occurs every day with no apparent increase in the eagerness of the parasites, until, after several days, they are suddenly noticed to be crowding on to the mine, over the spot where the Hispid lies. It is at this time that oviposition commences, and examination of

* The adult is described by Ferrière in *Stylops*, 2 : 97, 1933.

the mine, by holding it up to the light with the parasites on it, shows that the Hispid no longer attempts, as on previous days, to evade the parasites by wriggling rapidly along the mine as soon as it feels their ovipositors, and is, in fact, dead. It is therefore clear, firstly, that it is the mine which attracts the parasites initially; secondly, that a rather brief inspection of the mine suffices to dispel the attraction so long as the Hispid is alive; and thirdly, that when the Hispid is killed by the primary parasites the attraction is maintained and oviposition can commence.

The adult life is longer than that of any of the primary parasites. Accurate records were made for 17 females and 10 males, all being fed on honey in water and kept in glass tubes. The results were :—

| | | | |
|---|---|---|---|
| ♀♀ | Minimum, 19 days. | Maximum, 53 days. | Average, 33 days. |
| ♂♂ | „ 13 „ | „ 33 „ | „ 25 „ |

When the host is *D. javanica*, the maximum number of *A. orientalis* which can mature in one mine is equal to the number of *D. javanica* present. On the other hand, when the host is *P. painei* or *P. parvulus*, the maximum number of *A. orientalis* is always less than the number of primaries present, since if all the primaries are parasitised the secondary individuals reduce their own number by cannibalism.

As a general rule, when more than 12 individuals of *D. javanica* are present in one mine, *A. orientalis* does not succeed in parasitising all of them. The maximum number reared from one mine was 11, and 7 individuals of *D. javanica* emerged from this mine also, the total number of the latter species originally present being 18. When less than 12 *D. javanica* are present, *A. orientalis* frequently attacks all of them. It is probable that this difference is due, not so much to inability on the part of the parasite to discover all the primaries present, but rather to the fact that the number of mature eggs present in the ovaries of large females at any one time is limited to approximately 12, as was shown by dissections. If more than 12 individuals of *A. orientalis* emerge from one mine, as is sometimes the case with mines attacked by the internal primaries, it is probable that the mine was attacked by 2 females at approximately the same time.

When the host is one of the internal parasites, the maximum possible number of *A. orientalis* per Hispid appears to be in the neighbourhood of 25. The maximum number actually bred was 24, but 2 *P. parvulus* had previously emerged from the same host. This occurred on 2 occasions, the Hispid in the one case being a large 3rd-stage larva, and in the other a pupa. Within this maximum limit the number varies indefinitely. The minimum actually recorded for a large Hispid individual collected in the field was 3, and in this case 18 *P. parvulus* emerged also. For large Hispid individuals from which only *A. orientalis* emerged, all the primaries having been destroyed, the number varied from 7 to 18. In those rare instances where the number of *A. orientalis* exceeds 20, the total number of primaries originally present exceeds 30.

In the laboratory, *A. orientalis* was induced to attack parasitised pupae of two Hispids which are never attacked by it in nature. These two species were ***Bronthispa longissima***, Gestro, and ***Plesispa reichei***,

Chap., both of which feed as larvae and adults between unopened leaves of the coconut palm, eating only from the surface and never mining. The parasite which served as host was one which never attacks any mining Hispid, but is extremely abundant in West Java as an internal primary pupal parasite of these two Hispid species.

*A. orientalis* took no notice whatever of parasitised pupae of these two Hispids which were inserted into the glass tubes with it. But as soon as the pupae were put into mines of *P. nuciferae* whose normal occupants had first been removed, *A. orientalis* was immediately attracted to the mines and oviposited as readily in their abnormal occupants as it does in its usual hosts. Moreover, the progeny reached maturity absolutely normally, as regards both habits and rate of development.

d. *Life Cycle.* For the estimation of the duration of the early stages, 10 full-grown larvae of *P. nuciferae*, each containing about 20 prepupae of *P. parvulus*, were employed. The results are summarised below :—

| | |
|---|---|
| Incubation + internal feeding period . . | variable, 4– 6 days |
| External feeding period + prepupal period . | variable, 4– 6 ,, |
| Pupal period . . . . . . . | constant, 9 ,, |
| Total period, from oviposition to emergence of adult . . . . . . | variable, 17–20 ,, |

The records on which these figures are based were all obtained at Buitenzorg in October, 1932.

## G. The Natural Control of *P. nuciferae*, and the Relative Importance of the Parasites Concerned.

*P. nuciferae* occurs in all the provinces of Java, but is usually rare and local. It never becomes sufficiently abundant in Java to cause extensive damage, although it is occasionally common locally in a few adjacent trees. Its vertical distribution extends from sea-level to 1,500 ft., and possibly a little higher, and it is found inland as frequently as on the coast. Rainfall is a limiting factor in its distribution ; but the limits are nevertheless wide, and the insect is no more plentiful in East Java, which is relatively dry, than in West Java, which is wet. In nearly all localities it is unaffected by seasonal climatic changes. It appears to be unable to become permanently established in the very driest localities, such as the East Java coastal belt which includes Pasoeroean and Probolinggo, or in the very wettest, but between these limits, which embrace most of the areas where coconuts are plentiful, rainfall has no effect upon it. The rainfall limits for *P. nuciferae* appear to be about 60 ins. and 120 ins. per annum. Except in extreme cases, therefore, rainfall is not a controlling factor. In the extreme cases, the absence of the species is almost certainly due (cf. *P. reichei*) to the drying and hardening of the leaf tissues round small mines, on the one hand, and to the drowning of the larvae in their mines, on the other.

Except in very dry and very wet localities, the general rarity and local character of the species is due solely to the activities of natural

enemies. In Celebes, severe outbreaks occasionally occur, and in Borneo, the Philippines, and elsewhere, the closely allied *P. cumingi* occasionally occurs in severe outbreak form. The available evidence from these countries indicates that the outbreaks are due to the temporary suspension of the activities of parasites, and not to any climatic factor. The temporary suspension of the activities of parasites is due to the accidental introduction of the Hispid without its parasites into new localities. Many of these outbreaks occur in the drier regions of the countries concerned, and this at first suggests, quite erroneously, that they are due to lack of rainfall. In general, coconuts cover very much more extensive areas in the drier regions than in the wetter ones, and extensive cultivation greatly increases the chance of the pest being introduced into new localities without its parasites and also enables the pest to multiply and spread rapidly before the parasites find it. In addition, the lack of food-plants for alternative hosts of the parasites, wherever coconuts are extensively cultivated, prevents the parasites from being generally distributed and from reaching *P. nuciferae* in new localities. In Java, coconuts are abundant, but are not extensively cultivated. They are scattered all over the country, mainly in isolated groups in towns and native settlements, and the groups are widely separated by fields of rice, sugar-cane, and other crops. Where the coconuts grow, there are nearly always bananas also, and many other plants attacked by Hispids, and consequently the parasites of *P. nuciferae*, with the exception of *D. javanica* which has no other host, are very much more generally distributed than *P. nuciferae* itself. In these circumstances, and in view of the nature of the parasites, *P. nuciferae* can never be a pest, and it is, in fact, unknown as a pest in Java.

It is very evident in Java that the equilibrium between *P. nuciferae* and its parasites is unstable and wave-like. Wherever the pest is rare, parasitism does not exceed 50%; wherever it is common, parasitism is very high and always becomes total before many trees are affected and before any trees are severely damaged. The conditions are, in fact, exactly the same as they evidently were in the case of *P. reichei* in Fjii prior to the introduction of the mite *P. ventricosus* and the extensive cultivation of coconuts. But whereas the equilibrium between *P. reichei* and its parasites can be completely unbalanced, by the one-stage condition, so that *P. reichei* becomes a serious pest, the equilibrium between *P. nuciferae* and its parasites cannot be unbalanced because the one-stage condition is impossible, the oviposition period of *P. nuciferae* being so long that all stages are present after a single generation. This is a most important difference between the two species from the economic point of view. The multiple-stage condition is entirely favourable to the parasites, and outbreaks in which it prevails can only develop in the complete absence of parasites initially.

Extensive statistics concerning the percentage parasitism in Java were obtained from all parts of the country, but these proved to be of little value because the percentage is not constant in any one locality, the equilibrium being unstable. The percentage steadily increases, in each locality independently, until it reaches 100%, and observations made at any one time merely serve to indicate the time which must elapse

before the suppression of the pest is complete. The pest is never completely wiped out in any one locality, because 100% parasitism only occurs in trees in which it is common. In the neighbouring trees which are less severely attacked a few pest individuals survive, the percentage of pest individuals which the parasites are able to find being directly proportional to the degree of concentration of the pest. The survivors, however, are an extremely small percentage and the pest is reduced to a condition of great rarity. Since the suppression of the pest always occurs before any appreciable damage is done, and the equilibrium, although unstable, is always maintained, the parasites can be regarded as thoroughly efficient controlling factors.

The statistics obtained in Java, although unsuitable for estimation of the total control exercised except on those occasions when 100% parasitism was reached, served to show the relative importance of the various parasites concerned. In every locality in which *P. nuciferae* was found, sample leaflets were taken and all the eggs and mines, old and new, in the sample leaflets were separately examined and recorded. There is no advantage in expressing the numbers of individuals killed by the various parasites as percentages of the total present, because the samples taken contained individuals representing at least 3 generations, and it is not possible, when all stages are present as is the case with *P. nuciferae,* to determine by examination the age of the old eggs and mines with sufficient accuracy. In these circumstances, percentages have no meaning. It is, however, possible, from material collected in this way, to judge which of the parasites present are principally concerned in the control. In all localities except two, *A. promecothecae*, *D. javanica*, and *P. parvulus* were present together, and their relative abundance was always the same. No matter whether the pest was rare and just beginning to multiply, or whether it was common and about to be suppressed, *A. promecothecae* and *D. javanica* were always abundant, relative to the pest, and *P. parvulus* was always uncommon. It was always evident, when all three were present, that only *A. promecothecae* and *D. javanica* were controlling factors, *P. parvulus* being negligible; and that although 100% parasitism was finally reached by *A. promecothecae* and *D. javanica* jointly, either of these two species would be capable, by itself, of effecting satisfactory control. The rarity of *P. parvulus* in these conditions suggests that this species is incapable of multiplying more rapidly than its host, but this conclusion is entirely unsound. In two localities near Malang (Singosari and Sanan), which were the two exceptions to which we have referred above, *D. javanica* was absent and *P. parvulus* was found to be very abundant, and to have attained 100% parasitism in the living larvae and pupae collected, so that the pest was entirely suppressed. The secondary parasites were present as usual. These two instances were most important, because they proved, beyond doubt, that the rarity of *P. parvulus* in nearly all localities is due, not to any inferior capacity for multiplication or to the activities of secondary parasites, but to competition with *D. javanica*. Experiments showed that when both *P. parvulus* and *D. javanica* attack the same host individual at approximately the same time, *D. javanica* develops and matures, and *P. parvulus* dies. On account of the rapid growth of its larvae as external parasites, *D. javanica*

causes the death and destruction of the host while the *P. parvulus* larvae are still small, the latter being unable to live except in living hosts and unable to grow rapidly enough to compete with *D. javanica*. So long as both species are uncommon there is no appreciable interference, but as soon as *D. javanica* becomes abundant competition is keen and *P. parvulus* suffers. The control of the pest, however, is no less effective as a result of the competition.

In Java, therefore, there are 3 parasites which are separately capable of controlling *P. nuciferae*.* Of these, *A. promecothecae* and *P. parvulus* are invariably present, in the writer's experience, in every locality, and *D. javanica* is usually but not invariably present. Wherever *D. javanica* is present, it is the principal controlling factor, but where it is absent its place is efficiently taken by *P. parvulus*. *D. javanica*, although in general the principal factor, is the least sure because its presence cannot be relied upon. Its occasional absence is attributable to its failure to attack any Hispid other than *P. nuciferae*, and the invariable presence of the other two species is due to the fact that they have other hosts in other food-plants. The importance of alternative hosts in this respect is of special interest in connection with the serious outbreaks of *P. nuciferae* and *P. cumingi* which occasionally occur in other countries as a result of the extensive cultivation of the coconut palm and of the accompanying suppression of other plants which could provide hosts for the parasites. In Java, the accidental introduction of *P. nuciferae* into a new locality results in the absence of *D. javanica* only. In countries where coconuts are more extensively cultivated, it may result in the absence of all parasites.

It is noteworthy that the two secondary parasites, *P. detrimentosus* and *A. orientalis*, although invariably present and relatively common, never prevent the effective control of *P. nuciferae* by the primary parasites which they attack. There can be no doubt that if they were not present, *P. nuciferae* would be suppressed even sooner than it actually is, but since it does no appreciable damage in any case, the secondaries are to be regarded as economically negligible. The comparative rarity of *P. parvulus* in most localities is not mainly due to secondary parasites. *A. orientalis* is the principal parasite of *P. parvulus* in coconuts, but it does not greatly hamper the latter because in the majority of mines which it attacks it does not destroy more than 50% of the individuals present. *P. detrimentosus* is more common than *A. orientalis* as a natural enemy of *D. javanica*, but it obviously does not hinder it greatly. Both of the secondary parasites are unable to multiply rapidly until their hosts have become plentiful, and the required degree of abundance of the primary parasites is such that the suppression of *P. nuciferae* by them is effected before the secondaries are sufficiently numerous to prevent it. The almost complete disappearance of the primaries necessarily results from the suppression of *P. nuciferae*, so that the conditions become very unfavourable for the secondaries very soon after they have been thoroughly favourable.

* *P. painei*, *Polysphincta* sp., *Opius* sp., and *Cirrospilus* sp. are absent from most localities as parasites of *P. nuciferae*.

## H. The Selection of Parasites for Introduction into Fiji.

### 1. The Nature of the Problem in Fiji.

*P. reichei*, like *P. nuciferae*, is normally efficiently controlled by its indigenous parasites, and it can become a pest only when its indigenous parasites are prevented from multiplying normally. The duration of its oviposition period is very sbort as compared with that of its life cycle, and consequently the one-stage condition is possible and cannot be replaced for several months by the multiple-stage condition, which is the normal one and is ultimately inevitahle in normal circumstances. The parasites depend, for their economic efficiency, upon the multiple-stage condition, and are rendered economically useless by the one-stage condition, which prevents them from breeding continuously and causes them to die in large numbers periodically without progeny. The accidental introduction into Fiji of the mite, *P. ventricosus*, caused the one-stage condition to occur abnormally frequently, and to be maintained indefinitely in spite of the inherent tendency of the pest to overcome it, and consequently the parasites were rendered ineffective for abnormally long periods and severe outbreaks resulted. The problem of the control of *P. reichei* therefore resolved itself into the control of the one-stage condition, either by preventing its occurrence or by limiting its duration.

A thorough investigation of *P. reichei* in Fiji showed that there was no means of preventing the occurrence of the one-stage condition. One-stage outbreaks were found to arise from otherwise negligible multiple-stage outbreaks, and these in turn were found to be due to the separation of the pest from its parasites by factors which cannot be controlled. The transformation to the one-stage condition was found to be due to the mite, and the maintenance of that condition to be due to the mite and *O. utilis*, together with the short oviposition period of the pest which prevents an immediate return to the multiple-stage condition as soon as the mite is suppressed by wet weather. The mite cannot be controlled, and *consequently one-stage outbreaks cannot be prevented.* The only possibility, therefore, was to accept the occasional occurrence of the one-stage condition as inevitable and to seek some means of preventing its maintenance. Its occurrence is, in any case, not appreciably harmful, since the number of trees initially concerned is very small. Its indefinite maintenance, on the other hand, is exceedingly harmful, since the beetles can continue spreading indefinitely so long as it prevails. None of the factors concerned in its maintenance could be directly controlled, and the only possible method, therefore, was to attack the pest directly by parasites, with a view to stopping the outbreaks completely in the one-stage condition and before they could become sufficiently extensive to do any serious damage.

The investigation of the indigenous parasites in Fiji showed in what respects they failed, and suggested what type of parasite was required to succeed where they were useless. The most important fact revealed by the investigation was that there were no pupal parasites, except the mite which attacks all stages but operates only in the dry season. In multiple-stage outbreaks, the lack of a pupal parasite was not important, since

*Elasmus* and *Oligosita* could operate continuously and were capable, by themselves, of effecting complete control. In one-stage outbreaks, on the other hand, the lack of a pupal parasite meant that for the whole of the period of pupal predominance in every generation of the pest, there was nothing to reduce the pest population, except at those times when the mite could flourish. From the economic point of view, these periods were entirely wasted. A pupal parasite which attacked no other stages, however, would have to live an exceptionally long time, and in large numbers, to survive the very long period (about 3 months) when no pupae were present, and to have any appreciable effect upon the pest. It would have to survive much longer than *E. hispidarum*, since the pupal period of the pest is shorter than the larval period. It could survive either by living a very long time as an adult or by developing very slowly like *O. utilis*. In either case, however, it could not pass through more than one complete generation in one generation of the pest, the period of pupal predominance being short, and therefore, although it would assist in the control, it could not be expected to bring about complete control. These theoretical considerations clearly indicated that a purely pupal parasite would not be entirely satisfactory. Fortunately, however, there was a possible alternative, in the form of a parasite which would attack not only the pupae, but the larvae of all ages also. No such parasite was known, and there was a probability that none existed. parasites which attack both larvae and pupae of their host species, and at the same time are tolerably specific as regards their hosts, being comparatively rare. But the existence of such a parasite was by no means impossible, and there seemed every reason to believe that if it could be found it would be able to control one-stage outbreaks. It would be able to breed continuously throughout the larval and pupal periods of the pest, and would consequently be able, assuming its life cycle to be of normal duration for a tropical species, to pass through at least 3 generations in one pest generation and to multiply very rapidly relative to the pest. Moreover, as compared with *Elasmus* and *Oligosita*, it would have only a short time to wait before the larvae of a new generation would begin to appear, and provided that its adult life were not abnormally short it could be expected to survive this waiting period without suffering any appreciable reduction in its population. It would, in fact, be able to overcome all the principal obstacles which hinder *Elasmus* and *Oligosita*. A less serious obstacle, which we have not yet considered in this connection, is the existence in Fiji of natural enemies of the indigenous parasites, in the form of secondary parasites and *P. ventricosus* itself. Except in the case of the mite, it was impossible to foretell whether these natural enemies would attack an introduced parasite, but it was evident that the chances of their doing so would be minimised if the parasite selected differed greatly in habits from their normal hosts. *T. taylori* was the only purely secondary parasite to be feared, and its normal host, *E. hispidarum*, is an external parasite. There were no internal larval or pupal parasites of *P. reichei* in Fiji, and it therefore seemed probable that an internal parasite would not be subject to the attack of *T. taylori* to any great extent, if at all, the latter being primarily adapted to attack external parasites. The mite would certainly attack any introduced parasite if it could reach it, but the severity of its attack

would presumably be less in the case of an internal parasite, protected by the Hispid skin, than in the case of an external one.

It was necessary, in considering the type of parasite required, to bear in mind the peculiar way in which *P. reichei* spreads in one-stage outbreaks. It spreads from the original area of infection after about 4 generations and from every newly-infected area after 2 generations. Moreover, its spread occurs suddenly and at long intervals, so that at the time of spreading all natural enemies are left behind. It was not sufficient, therefore, that the parasite introduced should be able to control the pest within a given area. It must also be able to spread very rapidly, almost immediately after the pest itself spreads, to new areas. The parasite, if present at the very beginning of an outbreak, could be expected to bring the pest under control before spreading occurred. Its presence at the beginning of an outbreak, however, could not invariably be relied upon, since it would have no alternative hosts in most coconut areas in Fiji, and consequently it must be capable of overtaking the pest, if need be, after spreading has commenced and of suppressing it within 2 generations. To do this, it must be able to multiply with almost phenomenal rapidity, relative to *P. reichei*. The pest, however, multiplies comparatively slowly, having a very long life cycle and a very small egg-capacity. The rate of multiplication of the parasite, therefore, need not be abnormally rapid, since the relative rate, rather than the actual rate, is the important factor. It was safe to assume, judging from *Elasmus*, that the parasite would invariably find an outbreak by the time when maximum defoliation is first reached (*i.e.* within 4 pest generations), and nearly always much sooner. The potential pest population at the time is 16,500 (Table V), and after 2 more generations, when spreading is about to occur for the second time, it is $1\frac{1}{2}$ million. The parasite, therefore, must be capable of attaining a similar degree of abundance within the period covered by these two pest generations, if it is to be effective in all possible circumstances. A parasite with an egg capacity of 40 and numerical equality of the sexes, would attain a female population of about 160,000 from a single paired female in 4 generations, and about 3 millions in the next generation. This parasite could therefore control *P. reichei* in all circumstances, provided it could pass through 5 generations in 2 one-stage generations of *P. reichei*, or not less than 3 generations in one of the latter. Since the periods of larval and pupal predominance in one-stage outbreaks together cover 3 months (fig. 11), the parasite would be satisfactory if one generation did not cover more than one month.

Theoretical considerations of this kind are necessarily approximate only, on account of the multiplicity of the factors concerned. It does not follow that every parasite which agrees with the assumed conditions of egg-capacity, sex-ratio, and so on, would prove capable, in practice, of controlling the pest. On the other hand, considerations of this kind show definitely what parasites are useless, and for elimination purposes they are invaluable. Moreover, it is possible, provided that the egg-capacity, sex-ratio and life cycle of the pest are known, to fix a minimum value for the biotic potential of the required parasite for any given number of parasite generations per host generation. In the present case, the biotic potential (egg-capacity × sex-ratio) must not be less than about 20 (40 × 0·5), but

the actual values of the egg-capacity and sex-ratio are immaterial so long as their product is 20 or more. This is based on the assumption that the parasite can pass through 3 generations in one of the pest.

It is now convenient to list the various conditions which the hypothetical parasite would probably be required to fulfil in order to control *P. reichei* :—

i. It must attack the larvae of all ages and also the pupae.
ii. It must be internal.
iii. It must live, as an adult, for not less than 3 weeks.
iv. One generation must not cover more than one month.
v. Its biotic potential must not be less than 20.
vi. It must be very active and capable of rapid spreading.
vii. It must not be adversely affected by the climatic conditions of Fiji.

The selection of parasites to be introduced into Fiji was based upon these requirements.

### 2. Selection of Parasites to Fulfil Required Conditions.

The investigation in Java yielded only 4 parasites from which a choice could be made, and these were *D. javanica*, *P. painei*, *P. parvulus*, and *A. promecothecae*. Inspection of the mines in Java showed at once that *D. javanica* was abundant almost everywhere and indicated that it was capable, by itself, of controlling *P. nuciferae* completely. Its efficiency in Java would certainly have led to the conclusion that it was the right parasite to introduce, had not the very special uature of the problem in Fiji been very thoroughly understood. Similarly, the comparative rarity of *P. parvulus* and its obvious failure to play any appreciable part in the control in most localities, would have seemed to indicate that it could serve no useful purpose in Fiji. On the other hand, a thorough study of both parasites, in relation to the seven conditions which the species to be introduced was required to fulfil, showed that the one which was most valuable in Java, *D. javanica*, could in no way cope with *P. reichei* in one-stage outbreaks in Fiji, and that the much less common *P. parvulus* fulfilled the requirements remarkably satisfactorily and should, on theoretical grounds, prove most effective in Fiji. In view of the exacting nature of the requirements and the small number of parasites found, it was very remarkable that one of the parasites in the first country to be investigated should prove theoretically suitable. With the possible exception of the first, none of the requirements, considered separately, was particularly exacting, but the prospect of finding a Hispid parasite which would satisfy all of them together was very remote. The requirement that one generation should not cover more than one month was not precisely fulfilled by *P. parvulus*, although its life cycle in large host individuals is considerably less than one month. On account of the long duration of the oviposition period, the mean duration of one generation is considerably longer than the life cycle and covers rather more than a month. Compensation for this, however, was provided by the biotic potential, which was found to be very much greater than 20, mainly on account of the great predominance of females. The invariable presence

of *P. parvulus* in every locality in which *P. nuciferae* was found, even in very isolated trees in the centre of wide, windswept areas of rice fields, testified to its ability to spread; and the fact that it was to be found, unlike *D. javanica*, in the mountains as well as on the plains implied that the climatic conditions of Fiji would not affect it adversely. The effective control by *P. parvulus* observed in 2 localities in which *D. javanica* was absent showed that its comparative ineffectiveness in Java as a whole was no criterion of its economic ability.

*D. javanica* was found to be almost identical with *E. hispidarum* as regards habits, egg-capacity, life cycle, and sex-ratio. It would be certain, therefore, to be no more effective in one-stage outbreaks iu Fiji than *E. hispidarum* itself, and it might conceivably be more ineffective because, being confined to low elevations in Java, it might be adversely affected by the cool season climate in Fiji.

*P. painei*, being an internal parasite attacking pupae, was of special interest in view of the lack of pupal and internal parasites in Fiji. Its introduction into Fiji would complete the sequence of parasites, *O. utilis* and *E. hispidarum* attacking the eggs and larvae respectively. On the other hand, since it is a purely pupal parasite it would be useless in one-stage outbreaks, as it could not be expected to live long enough in bulk, if at all, to survive the long periods when pupae are entirely absent, and it could not pass through more than one complete generation in one generation of *P. reichei*. Further, it frequents bananas commonly, but coconuts rarely, and although it might conceivably have changed its habits in this respect in the absence of alternative hosts, the chances were that it would not do so.

*A. promecothecae* was obviously useless. It is mainly a parasite of eggs which are about to hatch, and eggs in this condition are present for only about 2 weeks in each pest generation in one-stage outbreaks. The parasite therefore could not pass through more than one generation in each one of the pest. Moreover, since its life cycle covers about 3 weeks only, as against 7 weeks in the case of *Oligosita*, and its adult life is not abnormally long, it almost certainly could not survive the very long periods when no eggs are present.

When a thorough understanding of the habits of these 4 Java parasites had been obtained, *P. parvulus* was definitely selected for introduction into Fiji as being the most likely to bring *P. reichei* under control. Attention was then paid to methods of breeding it in bulk and of dealing with it on board ship during a long voyage. It was evident at the same time that although *D. javanica* and *P. painei* appeared very unlikely, on theoretical grounds, to serve any useful purpose, their introduction could not be in any way harmful; and it was therefore decided that these 2 species should be introduced with *P. parvulus*, mainly to test the soundness of the arguments upon which the selection of *P. parvulus* had been based. If *P. parvulus* had not been found in Java, the introduction of these other parasites could not have been justified, and it would have been necessary to extend the search to other countries.

*P. parvulus* was most successful in Fiji (Section VIII), and the theoretical considerations, upon which its introduction and the abandonment of plans for furtber search were based, proved entirely sound; the other

two species proved as useless in one-stage outbreaks as they were expected to be, and the failure of *D. javanica* in particular was a striking demonstration of the futility of judging the suitability of a parasite, for controlling an insect in another country, from its economic importance alone in its own country. The suppression of *P. parvulus* in Java resulting from competition with *D. javanica* can only occur when all stages of the host are present simultaneously. It was likely to occur in Fiji in multiple-stage outbreaks if *D. javanica* became established; and even if *D. javanica* did not become established, *E. hispidarum* was likely to have the same effect. This, however, was immaterial, because *P. parvulus* could not be eliminated by competition, and as soon as one-stage outbreaks occurred, it would take control as effectively as *D. javanica* or *E. hispidarum* do in multiple-stage conditions.

## VII. *PLEUROTROPIS PARVULUS*, FERR. (EULOPHIDAE.)

### A. HOSTS.

In Java, *P. parvulus* attacks *P. nuciferae*, *G. xanthomelana* (in bananas and Zingiberaceae), and *G. taylori*. It is most commonly found as a parasite of *G. xanthomelana* in bananas, but this is due to lack of competitive external parasites in the banana mines and not to any tendency on the part of the parasite to frequent bananas more than any other food-plants of its hosts. It does not attack Hispids mining in bamboos, rice, or other grasses.

When it was introduced into Fiji, it attacked *P. reichei* as readily as it attacks its normal hosts in Java. It also attacked, and matured in, *P. bicolor* in the laboratory, and there is little doubt that *P. bicolor* will be attacked in its natural habitat in the forests also. In Fiji, there are no insects, other than *P. reichei* in coconuts and *P. bicolor* in *Flagellaria* spp., which can serve as hosts.

### B. DISTRIBUTION.

*P. parvulus* is known from Java only. In Java it is very generally distributed, from the dry eastern end to the wet western end. The general distribution of *G. xanthomelana* is largely responsible for that of the parasite. *P. parvulus* is to be found in the forests as well as open country, and its vertical distribution extends from sea-level to about 4,000 ft.

### C. DESCRIPTION OF STAGES.

1. **Egg.** (Fig. 15.)

The egg is elongate and its long axis is curved. The anterior end is considerably wider than the posterior, and the greatest width is at about one-third of the length from the anterior end. The micropyle is visible as a minute thickening at the anterior pole. The egg is entirely without appendages and is colourless, smooth, transparent, and very shiny. Its size is nearly constant and does not vary with the size of the female parasite. The length is approximately 0·2 mm.

2. **Larva.** (Fig. 15, and Plates II and XXII.)

The newly-hatched larva (Fig. 15) is colourless and transparent. The skin is very fragile and is entirely smooth and without setae or any other surface structures. The anterior end is broadly rounded; the greatest width is at the 4th segment, and the body tapers regularly behind this segment to the rounded, but much narrower, posterior extremity. There are 12 well-marked segments, in addition to the head segment which is large and is not separated by a constriction from the first body segment.

The head and the first two body segments are considerably longer than any of the following segments, all of which are approximately equal in length. The body is permanently curved towards the ventral surface. The mouth, which is slightly ventral, the oesophagus and the gut are clearly visible, but otherwise no internal organs can be seen clearly in the living larva. The mandibles are short, sharp, points, and, being only slightly chitinised, are nearly colourless. There is no trace of a tracheal system, respiration being wholly apneustic, and the anus is not perforated. The length of the newly-habited larva is 0·22 mm.

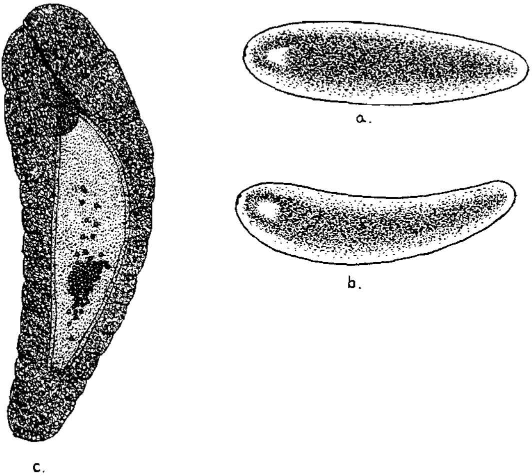



FIG. 15.—*Pleurotropis parvulus*; a and b, egg, dorsal and right lateral as seen by reflected light (× 280); c, newly-hatched larva, left lateral, as seen by transmitted light without compression (× 410).

The fully-grown 1st-instar larva (Plate XXII) is very different in appearance from the newly-hatched larva. The gut, which is now bright yellow on account of the absorption of the body contents of the host, occupies the greater part of the body, from the 2nd segment to the 10th, inclusive. In the newly-hatched larva, the head is comparable in size and appearance to the body segments, its outline forming a continuous curve with the latter; but at the end of the 1st instar the head is merely a minute papilla on the antero-ventral face of the 1st segment, which is now considerably larger than any of the other segments (Plate XXII). The change in

appearance of the head, relative to the body, is due to the fact that the body grows enormously but the head does not grow at all. In this and in all later instars, therefore, the size of the head is a certain indication of the instar. In the fully-grown 1st-instar larva, the posterior segment projects posteriorly and dorsally in a small lobe, which possibly represents a 13th segment.

The mean length of the larva at the end of the 1st instar, and when fully extended, is 0·44 mm., and the width of the head throughout the 1st instar is 0·034 mm.

There are 4 larval instars. The general form and appearance of the larva is the same in all instars. Immediately after each moult the head is large and comparable to a body segment, but at the end of each instar it is small and button-like. Except at the end of each instar, the shape of the larva varies very greatly, since it is capable of extensive expansion and contraction. At the end of each instar, however, just before the moult, the skin is very tightly distended, so that the segmentation is not clearly visible, and in this condition the larva is incapable of extensive change of shape. The head widths in the 2nd and 3rd instars are respectively 0·11 mm. and 0·17 mm., and the mean lengths of 2nd and 3rd-instar larvae, at the ends of the instars, and when fully extended, are 0·82 mm. and 1·22 mm. respectively. The maximum length attained and the size of the head in each of the first 3 instars is nearly constant, regardless of the size of the host and the number of parasites per host; but the corresponding dimensions in the 4th (last) instar are liable to considerable variation. The maximum length of the full-grown larva is 2·52 mm., and this, approximately, is the length usually attained when the number of parasites per host is not greater than usual for the size of the host. The corresponding head width is 0·24 mm. When the number of parasites per host is abnormally high, however, the dimensions of the larvae, when full grown, may be much less.

The tracheal system first appears in the 3rd instar, the main tracheal trunks appearing at the 2nd moult. In the 3rd instar, however, the tracheal system is very incomplete. Only the main tracheae are present, and there is never any trace of spiracles. The presence of tracheae without spiracles affords a very useful means of recognising this instar, the tracheae being readily visible through the transparent skin. The complete tracheal system is present throughout the 4th instar, appearing at the 3rd moult. It cannot begin to function until towards the end of this instar, however, since the larva is surrounded by fluid until it is fully grown. The distribution of the spiracles is peculiar and irregular (Plate XXII). There are occasionally 7 pairs, but never more than 7, and usually these are asymmetrically arranged; that is to say, some segments have 2 spiracles, some have 1 only, and some have none, and although there are often 7 on one side of the larva there are almost invariably less than 7 on the other side. The full complement is 7 pairs—on segments 2, 5, 6, 7, 8, 9, and 10. Segment 2 is the only one which invariably has 2 spiracles, and segments 1, 3, 4, 11, 12, and 13 are always without any. Some larvae have only 3 spiracles on one side, but in such cases there are always at least 5 on the other side. In internal parasites, irregularity in the spiracles is not unusual, but in *P. parvulus* it is extreme.

The 4th instar, although similar in general form and appearance to the earlier instars, differs from them in certain respects other than the presence of spiracles. These differences are that in the 4th instar the greatest width is at about the 8th segment, the 13th segment is clearly demarcated, the points of the mandibles are strongly chitinised and brown, and the skin, while still very shiny, is slightly less smooth just after the moult because on each segment there are minute surface reticulations across the back and down the sides. The reticulations are only visible just after the moult, the skin later becoming as smooth as in the earlier instars. The full-grown larva, like the earlier stages, is entirely without setae, microtrichia, or any other surface features. The shape of the mandibles and the extent of chitinisation in them are shown in fig. 16. The head bears 2 pairs of extremely minute papillae, representing antennae and palpi.

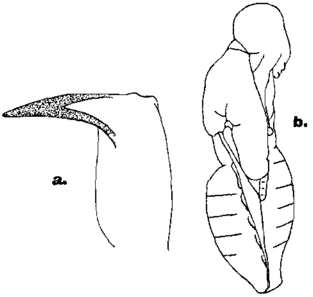



FIG. 16.—*P. parvulus*; a, mandible; b, outline of pupa, right lateral.

3. **Prepupa.** (Plate XXII.)

The prepupa (*i.e.* the 4th-instar larva after excretion) is pure white, opaque, and shiny. The thoracic segments are much larger than the abdominal, but the body is widest in the abdomen. The head is small and nearly hemispherical. It is situated on the antero-ventral face of the 1st segment. The skin on the abdomen and on the metathorax dorsally is greatly wrinkled transversely; but on the head and the first 2 thoracic segments it is extremely smooth.

4. **Pupa.** (Plates XIV and XXII, and Fig. 16.)

The pupa is black, opaque, and exceedingly shiny. It has a slight blueish sheen. Its stout, compact, form, its general shape, and the blueish sheen, together serve to distinguish it from all other species which are to be found in the mines in Java or Fiji. The outline of the ventral thoracic plate (fig. 17) is characteristic also (cf. *P. painei*, etc.). The size

of the pupa varies considerably, according to the number of individuals per host and the size of the host, but the mean length is 1·56 mm.

**5. Adult.** (Plates XXI and XXIII.)

The adult has been described by Ferrière (*Stylops*, 2 : 95, 1933). The males are always much smaller than the females of the same batch, and this, together with the fact that the thorax of the male, unlike that of the female, has a brilliant golden or bronze gloss ventrally, serves to distinguish the sexes readily even when the insects are alive. The usual sexual dimorphism in the antennae and external genitalia is readily apparent also.

## D. Life History.

**1. General.**

*P. parvulus* is an internal parasite. The egg, larval, and pupal stages and the early part of the adult stage are spent wholly within the host. It

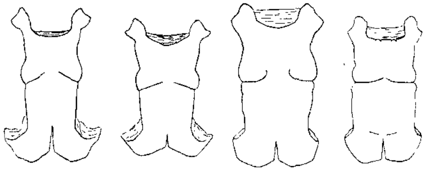



Fig. 17.—Ventral thoracic plates of pupae of a, *P. parvulus*; b, *P. detrimentosus*; c, *A. orientalis*; d, *P. painei*. (Outlines only.)

is never a secondary parasite. The host may be a 1st, 2nd, or 3rd-instar larva, a prepupa, or a pupa, and all these stages are attacked equally readily by the adult parasite, regardless of the species of host concerned. The attack of the adult parasite is, in itself, in no way detrimental to the host, which continues its development for some days. The host is eventually killed by the parasite larvae within it. In a single host individual many eggs are laid, and many parasites can mature.

*P. parvulus* can mature in host individuals attacked at any time from the hatching of the egg until 3 days before the adult beetle is due to emerge from the pupa.

**2. Egg.**

The eggs are laid inside the body of the host, the ovipositor of the parasite being inserted through the wall of the mine and the skin and body-wall of the host in one operation. The eggs are placed in the body-cavity of the host, between the body-wall and the gut. In this situation they are entirely immersed in the copious, clear, yellow, body-fluid. They are not attached in any way and in most cases they are constantly kept in motion by the movement of the fluid itself, which results from the normal activities of the host. Not infrequently, however, they are

deposited in the fat-body, in which case they are prevented from moving. The female parasite lays its eggs in any part whatsoever of the body of the host, but when the host is a larva there is a tendency for the eggs to shift gradually, as the host moves, to the posterior extremity of the body, where they collect around the rectum. This shifting is due partly to the bulkiness of the fat-body and the size of the gut in the more anterior segments, the resulting pressure diminishing towards the posterior extremity, and partly to the peristaltic movement of the gut wall. In young larvae, the skin of which is more transparent than that of older larvae, the shifting of the eggs can often be watched under the microscope. When the host is a pupa, however, there is no tendency for the eggs to collect in any particular region of the body. The tendency for the eggs to collect at the hind end of larval hosts is very useful when large numbers of larvae are being dissected for estimation of the extent of parasitism. The larva to be examined is placed in a drop of water upon a glass slide and punctured posteriorly with a needle. If it contains eggs, these are usually expelled immediately, and with considerable force, through the puncture. If eggs do not emerge the larva may nevertheless be parasitised, since eggs situated anywhere but at the hind end remain *in situ*. In this case, a normal dissection must be made and the body contents very carefully examined, but the eggs are very difficult to detect in these circumstances.

The stage of development of the embryo within the egg is readily visible through the chorion.

3. **Larva.**

The larva splits the chorion of the egg anteriorly only, and emerges into the body-fluid of the host. The egg-shell, which necessarily remains within the body-cavity of the host, can very rarely be found, its minute size and extreme transparency rendering it invisible. In many species of internal parasites the egg-shell remains attached to the hind end of the larva, but in ***P. parvulus*** it is almost invariably shed completely. The larva moults 3 times as it grows, and the cast skins are usually discarded completely, like the egg-shell.

The young larvae, even more than the eggs, tend to collect at the hind end of the host, because those which emerge from eggs entangled in the fat-body free themselves from the latter and are gradually forced backwards. The larvae cannot be said to migrate, however, the shifting being due solely to pressure from surrounding bodies. Older larvae are situated in any part of the host body. Growth is comparatively rapid, and the larvae soon become too large for all of them to be accommodated at the posterior extremity. The larva is entirely incapable of rapid movement, and, indeed, the only movements of which it is capable at any stage of its growth are a slow and slight wriggling and slow but extensive contractions and expansions. When it is very small, these movements do not result in any change of position relative to the parts of the host body, but as soon as it becomes large enough to come in contact at several points with the body-wall or organs of the host, these slight movements automatically cause a gradual change of position. The result is the distribution of all the larvae present to all parts of the host body. This shifting,

however, like the initial shifting to the posterior extremity, cannot be regarded as migration, since it is not directional and is not a response to any stimulus except to the extent that the larvae are forced forwards at first by their own growth.

Except during the moulting periods, the larvae feed incessantly. Moulting is a rapid process and involves cessation of feeding for 6 hours only.

During the first 3 instars the larvae feed solely upon the copious body-fluid in which all the organs are bathed and by which the skin is distended. Throughout this time the host pursues its ordinary activities, and its internal organs, including the voluminous fat-body, remain perfectly normal. The mandibles, apparently, do not function during this period, and this view is supported by their fragility and lack of chitinisation. As soon as the parasites reach the 4th instar, however, they begin devouring all the internal organs, their mandibles having become strongly chitinised at the 3rd moult in readiness for this attack. The muscular and nervous systems are attacked early in this instar, and this causes the host to become lethargic and soon to die. Eventually all the organs are completely destroyed, the fat-body and gut being devoured last. If the host is a larva the contents of the gut are expelled through the anus as it dies, before the gut is attacked by the parasites. The emptying of the gut is due partly to the contraction of the muscles at death and partly to pressure upon its walls by the parasite larvae, which are now large and almost completely fill the host skin. Ultimately nothing but the skin remains.

It is at this time that the parasites first begin to breath air through the spiracles. Air enters the host skin and occupies the spaces between the larvae as they devour the last remains of the semi-liquid body-contents, and this takes place about 36 hours after the death of the host. The parasite larvae are now tightly packed together within the host skin, causing it to bulge here and there, and to be tightly distended, so that, except for the bulges, it retains its normal form. The full-grown larvae are extremely lethargic and are incapable of any movement except slow contractions and expansions; in any case, they are packed so tightly that any more extensive movement would be impossible.

As a result of the entry of air, the host skin begins to dry and harden, and as it does so one or two minute fractures or punctures usually appear. Fractures are due solely to pressure from within, and only occur when the parasites are excessively numerous. Occasionally a larva partly projects through such a fracture. Punctures are made by the mandibles of the larva, and it seems that unless fractures or other openings occur the larvae puncture the host skin to ensure a sufficient supply of fresh air. In very many cases, however, no punctures or fractures can be detected; and it is probable that none is made, the spiracles in the host skin remaining sufficiently open in these cases, so that there is no stimulus for puncturing the skin. The initial entry of air definitely takes place while the host skin is intact, presumably through the spiracles, but it seems probable that the spiracles alone often cannot permanently suffice. The skin of a *Promecotheca* larva is thick and very tough, and that of a pupa, though not tough, is chitinised and hard; in either case it would seem impossible for

air to penetrate except through a definite aperture. It is possible that the mouth as well as the spiracles sometimes remains open, but the anus is permanently sealed by the fluid which is expelled at death aud which hardens soon afterwards.

The parasite larvae excrete against the inside of the host skin or against one another, the excrement being deposited in separate drops which form a single mass for each larva. The excrement is in the form of a viscous, brownish-yellow, fluid, and each drop partially solidifies as soon as it is expelled, with the result that the mass finally produced is lumpy and lobed, although not divided. After about 4 days, and after pupation has taken place, the excrement becomes absolutely dry and exceedingly hard, and by this time the host skin also has dried and become hard and very brittle. The prepupal stage, which is not a separate instar, begins with the act of excretion.

4. **Pupa.**

Pupation takes place within the host skin (Plate XXIII), and never in any circumstances outside it, although the larvae, if artificially removed, pupate quite normally. The old larval skin persists in the form of a minute, white, twisted, tape, which is attached at one end to the excrement and at the other to the posterior extremity of the pupa. The pupae, when first formed, are white and soft, but within 8 hours they assume their permanent colouring and hardness. They are incapable of any movement of any kind, since the abdominal segments and the appendages are not movably articulated. The pupae are packed together without any regularity of arrangement or direction.

5. **Adult.**

a. *Emergence from the Pupae, and from the Hosts and Mines.* All the parasites within one host emerge from the pupae at approximately the same time, within 6 hours, the pupal skins being fractured anteriorly and ventrally. The adults then remain motionless within the host skin while their integuments harden. Emergence from the pupae takes place at any time during the day or night, and the subsequent hardening of the integument occupies approximately 12 hours. At the end of this time, the parasites are ready to escape from the host skin and from the mine, but they often remain motionless in the host for longer than 12 hours because they become active, preparatory to escaping, only in the early morning. Thus, if they emerge from the pupae at dawn on a certain day they become active within the host at dawn on the following day; alternatively, if they emerge from the pupae in the evening of a certain day they likewise become active in the early morning of the following day.

Emergence from the host and the mine is a somewhat lengthy process, occupying at least 2 hours and usually 3 hours. The parasites first bite ragged holes, just large enough for them to crawl through, in the host skin (Plate XXIII). The number of holes made in the host is always much less than the number of parasites present, the majority of the parasites utilising holes made by others, except when the host is a very small larva in which case the number of parasites present seldom exceeds 2 and is often only 1, and the number of holes often equals the number of parasites.

In large hosts (larvae or pupae), there are most frequently 3 holes, but the number varies from 1 to 6, and both 2 and 4 are of common occurrence. The holes are situated in any part whatsoever of the host, whether the host is a larva or a pupa. *P. painei*, on the other hand, seldom makes more than one emergence hole and always makes it at the posterior extremity of the abdomen of its pupal host. This specific difference, which is very remarkable, is useful, together with the pupal skins of the parasites, as a means of determining what species of parasite has attacked pupae from which the parasite individuals have already emerged.

On biting through the host skin, the parasites usually find themselves free in the mine, but it often happens that one or more of the holes which they make in the host skin are in a part of the latter which is in contact with the wall of the mine, in which case the parasites are never free in the mine. In either case, they begin biting through the wall of the mine immediately. The holes which they now make are almost invariably situated in the upper epidermis of the leaf, which is very much thinner than the lower, but holes are occasionally made in the lower epidermis. These holes, unlike those in the host skins, are neat and circular (Plate IX). They vary in number from 1 to 6, but are, in general, slightly less numerous than those made in the corresponding hosts. In large mines there are nearly always at least 2 holes. The parasite works at the bole in the mine almost incessantly, but nevertheless the process usually occupies 1½ or 2 hours. From time to time it thrusts its head into the aperture, testing its size. The holes may be made by either sex, but invariably the males, which are much less numerous than the females, escape from the mine either first or amongst the first. This is due to the fact that the males, unless they have already begun to bite holes for themselves, jostle the females and utilise the holes which the latter have made, the males, which are always smaller, being able to escape through apertures which the females require to make still wider.

Emergence from the mines almost invariably takes place between 7.0 and 10.0 a.m. The majority emerge about 9.0 a.m., having taken about 3 hours to escape after becoming active at dawn.

b. *Pairing and Parthenogenesis.* Pairing takes place as soon as the parasites emerge from the mine, but never inside the mine. Each male waits at one of the holes in the mine and pounces on a female immediately it appears. Pairing occurs at once, lasting about half-a-minute, and the male then returns to the hole to await another female. Often, some of the females emerge in rapid succession while the males are away from the holes in the mines, so that pairing cannot take place immediately. These females never leave the leaf at once, however, but merely wander round to the underside of it and there await the males, which, after waiting for a further period at the holes, this time without result, run over the leaf in a rapid and erratic manner in search of females with which they have not yet paired.

In consequence of these habits, almost all the females are impregnated as soon as they escape from the mines, and this is the normal habit. In small mines, however, there is sometimes only one parasite, and in these circumstances there is usually no male present when the parasite emerges. Pairing can, however, occur at any time during the lives of either sex,

and almost all females are impregnated sooner or later. Parthenogenesis, which produces males only, provides evidence for this; for although it occasionally happens that all the parasites from a large host collected in the field are males, this is an exceptionally rare occurrence. In the laboratory, unpaired females oviposit very readily but can only be obtained by immediate isolation on emergence, pairing otherwise taking place as in the field and invariably resulting in a great predominance of females in the progeny.

c. *Feeding.* The adults of both sexes feed on liquids only. They were observed in Fiji upon the nectar of coconut flowers, at the time when they became extremely abundant while suppressing outbreaks of *P. reichei.* They were also observed sucking up drops of dew in the early morning, but they do not live long if provided with water only. There is little doubt that the flowers of the food plants of their hosts provide their normal food and that they do not ordinarily visit other flowers. It is probable also that they feed upon exudations from the trunks or stems of the plants which they frequent, except the banana. Unlike certain other parasites of *Promecotheca* spp., they never bite through the mines and suck the body-fluid of the larvae. In the laboratory they lived and oviposited most satisfactorily, and apparently quite normally, when fed with drops of honey very slightly diluted with water. If provided with more dilute honey or moist lumps of sugar, they did not live so long.

d. *Locomotion and Degree of Activity.* The adults crawl and fly rapidly, and use both means of locomotion equally commonly. Their flight is powerful, due allowance being made for their minute size. Wind, except when very strong, does not appear to hamper their flight or to direct it. They take wing with a powerful initial jump, which propels them into the air at a speed such that the eye cannot follow them. Both sexes are extremely energetic and active, and their energy is associated with their robust build. All their activities are diurnal, however. At sunset they invariably withdraw to the darkest and most sheltered place they can find, and this is commonly the axil of a coconut leaf or the underside of a coconut leaflet at the junction with the main stem. They remain motionless throughout the night, but become active again at dawn.

The remarkable speed and uniformity of the spread of this species in Fiji, regardless of the prevailing wind and natural barriers, afforded striking evidence of its high degree of activity and extensive powers of locomotion.

e. *Response to Light and Heat.* The females are very strongly attracted by daylight. If released in a room, they fly straight to the nearest window. If a large number of them are enclosed in a glass tube, they all crowd at the lighter end, and if the tube is reversed, they all immediately crawl very rapidly to the other end. They are, in fact, more strongly heliotropic than any other parasite with which the writer is acquainted. The males, on the other hand, although not negatively heliotropic, do not respond nearly so readily as the females. This affords a simple means of segregating the sexes when very many are enclosed together in glass tubes, for if the open end of an empty tube is placed against that of a tube containing the parasites, the empty tube being towards the light, the females immediately enter it and the males remain behind.

Bright artificial light, at close quarters, causes the parasites to become

active at night, but they are never attracted to artificial light in the field.

The parasites are most active on hot, sunny, days, the temperature being almost as powerful a stimulus as the light. On cool days, however bright the sun may be, they are noticeably less active, and on cold, dull, days they are relatively lethargic, though not inactive. In bright light, the maximum activity occurs at about 95° F. The cool season in Fiji, although resultiug in diminished activity, was not in any way detrimental to them. This was to be expected, in view of the extensive vertical distribution of the species in Java.

f. *Duration of Adult Life.* In the laboratory, the majority of females live 6 weeks, but the duration of life varies greatly, from 3 weeks to 61 days (maximum). In general, the life of females which were constantly provided with mines in which to oviposit was rather shorter than that of females which were given no opportunity to oviposit. There were, however, many exceptions to this rule, and several females which were constantly giveu mines, and oviposited to their full capacity, lived for more thau 50 days.

It was possible in Fiji to confirm these laboratory records by direct observation in the field in one-stage outbreaks. In August, 1933, at Nabavatu, the predominant stage of the pest was pupae. Towards the end of the month, *P. ventricosus* multiplied with its usual rapidity and by September 1st not oue living pupa could be found. Mauy adult beetles emerged, however, before parasitism by *P. ventricosus* became total, and eveu on August 28th healthy pupae were still common. Wholesale destruction of all pest individuals except adults, and with them all parasite individuals except adults, took place at the very end of August. *P. parvulus* was destroyed with its host, and very few adults emerged after September 1st. The adults which did emerge had nothing in which to oviposit until the *P. reichei* eggs of the next generation began to hatch, and this occurred at the very end of September. The parasites oviposited abundantly in the young larvae which thus became available, and continued to do so until about October 9th, when bulk oviposition abruptly ceased, as was shown by dissections of hundreds of larvae, and nearly all the parasites died. Thus, the adult life of the majority of the *P. parvulus* females covered the period September 1st–October 9th, or roughly 5½ weeks.

The males live approximately 4 weeks, but seldom longer, and are nearly always outlived by the females.

g. *Oviposition.* Oviposition is effected from the underside of the leaf, and the ovipositor is thrust through the wall of the mine and into the contained larva or pupa.

In describing the habits associated with oviposition, it is convenient to assume that the host is a feeding, 3rd-instar, larva. The parasite, when about to oviposit, wanders over the under surface of the mine for a long time before it finally selects a spot at which to insert its ovipositor. During this preliminary survey it moves slowly, incessantly swaying from side to side and tapping the leaf surface with its antennae. It is able to distinguish between the mined and the healthy tissue, and whenever it moves beyond the edge of the mine it turns back; but it has great

difficulty in locating the position of the contained larva and passes over it many times without recognising its presence. From time to time it inserts its ovipositor into the mine, and usually many insertions are made at points far removed from the larva before the right place is found. In fact, while the mine attracts the parasite strongly and provides the initial stimulus for oviposition, the larva is detected by a process of trial and error, the parasite moving further along the mine after each abortive attempt. The larva is invariably located sooner or later, however, even though the preliminary survey often occupies half-an-hour.

When it has located the larva, the parasite inserts its ovipositor through the wall of the mine several times and touches the larva without penetrating the skin. On each occasion the ovipositor remains within the leaf for a considerable time, but no eggs are laid and the larva, which continues feeding, clearly does not feel the ovipositor. These operations appear to serve only to ascertain whether the prospective host is suitable (*i.e.* whether it is alive or dead, and whether it is healthy or parasitised). The parasite is able, when it chooses, to penetrate the skin in any region of the body, and there is therefore no reason to suppose that these operations are attempts to locate any particular place.

*Eventually, the parasite selects a point at which to oviposit.* The ovipositor is initially inserted in the same manner on this occasion as on previous ones, but whereas, at all the previous insertions, the ovipositor is thrust for only about half its length into the leaf, on this occasion it is thrust in as far as possible, and this is always an indication that oviposition is actually taking place. The parasite first curves its abdomen towards the leaf so that it is almost at right angles to the surface, and in order to do this it has to straighten its legs almost to their limit of extension. The abdomen then vibrates rapidly up and down, so that its extremity rapidly taps the leaf, and at the same time the extremity is moved slightly over the leaf surface. This process appears to serve merely for finding the *point, presumably one of the stomata, at which the leaf tissues can be most* easily penetrated. In a few seconds a suitable point is found, and the tip of the ovipositor is then inserted and the abdomen resumes its normal position. Hitherto the abdomen has served as a guide for the ovipositor, but the latter now projects from it almost at right angles. The penetration of the leaf epidermis is never followed by a sudden thrust of the ovipositor into the larva. Instead, the ovipositor is pushed in extremely slowly; so slowly, in fact, that the movement is much slower than that of the hands of a watch and is quite imperceptible. This ensures that the larva should not feel the ovipositor and move away. First the tip comes in contact with the skin of the larva; then, very slowly, a dent is made in the skin, the dent becoming deeper as the pressure increases; and finally, the point of the ovipositor makes a minute hole and the ovipositor is pushed right through the hole, still very slowly, until it can be thrust no further. The eggs are then laid, the ovipositor remaining inside the host for 2 or 3 minutes. The very gradual insertion of the ovipositor is effected by the gradual bending of the legs.

This method of oviposition is extremely interesting when compared with the more usual method, which is a sudden stab. The larva attacked by *P. parvulus* is entirely unaffected, as a rule, and continues feeding the

whole time. Sometimes, however, the larva chances to move to a new position for feeding, and when this happens it feels the ovipositor and immediately withdraws down the mine. The parasite then begins the whole process again, but in most cases it succeeds, by stealth, in laying its eggs inside the host without the latter being disturbed.

The ovipositor is withdrawn quite suddenly, since it is now immaterial whether the larva moves or not. Usually the larva feels the withdrawal, ceases feeding, and moves backwards along the mine, but it resumes feeding soon afterwards. In no circumstances is the host paralysed, and in nearly all cases all the eggs are laid at one insertion of the ovipositor. *P. painei* differs strikingly from *P. parvulus* in these respects. The attack of the former always results in the paralysis of the host, and each egg is laid with a separate insertion of its ovipositor. Moreover, the initial attack of *P. painei*, as well as each subsequent attack, is a sudden stab.

No puncture can ever be detected in the leaf after the withdrawal of the ovipositor, but on the skin of the host a minute shiny spot can usually be detected with difficulty. This spot is due to the exudation and subsequent drying of a minute drop of the body-fluid and is the same in pupae as in larvae. *P. painei* causes many conspicuous black spots, one at each point of insertion of the ovipositor. *P. parvulus*, as a parasite of pupae as well as larvae, causes a single minute spot, which is almost imperceptible and is never dark in colour. It is interesting to note that even when *P. parvulus* is artificially induced to attack a pupa which has already been punctured and paralysed by *P. painei*, no conspicuous black spot appears at the new puncture. This suggests that the conspicuous spots produced by *P. painei* are due to its habit of attacking the host with a sudden stab and are not associated with the paralysed condition of the host.

When the individual attacked by *P. parvulus* is a pupa, a moulting larva, or a small larva, the activities of the parasite are the same in all essentials as those which we have described for the case of a feeding, 3rd-instar. larva. In the case of a pupa or a moulting larva, however, the location of the host is usually more rapid, although the host is in the central part of the mine and not at the end. This appears to be due to the fact that in this case the leaf epidermis over the host is dead, whereas the epidermal tissue over a feeding larva is still alive. It is always noticeable that the parasite, when making its preliminary survey, can at once recognise the edges of the dead parts of the mine, but cannot readily distinguish the green epidermis at the end of the mine from the healthy, unmined, epidermis of the rest of the leaf. It is the dead tissue which attracts most strongly, and consequently it locates pupae and moulting larvae more rapidly than feeding larvae. When the attacked individual is a 1st-instar larva and is feeding, its position is located fairly soon, but this is simply because the mine, and therefore the area to be surveyed, is very small.

h. *The Number of Eggs laid, and the Number of Parasites that can Mature in One Host Individual.* The number of eggs per host was studied with *P. reichei* and *P. nuciferae* as hosts. No detailed investigation of this point was made with *G. xanthomelana*, but in general the account which follows applies to all host species.

The parasite invariably suits the number of eggs laid to the size of the host. When hosts are constantly available throughout the life of the parasite, the number laid is seldom in excess, and never greatly in excess. of the number of larvae which can mature in the host. A parasite which is very eager to lay, however, through having had no opportunity to oviposit for several weeks (as at certain times in one-stage outbreaks of *P. reichei*) is liable to oviposit excessively in early 1st-instar larvae, though not in larger ones or pupae; but even in these circumstances the number of eggs laid in the small larvae is very much less, on the average, than in large individuals.

The number of eggs normally laid in early 1st-instar larvae varies from 1 to 4 and is usually 3. When the females are very eager to lay, however, the number varies from 1 to 10 and the average is 5.* The maximum number of parasites which can mature in 1st-instar larvae (*i.e.* in larvae which are attacked so early that they do not reach the 2nd instar) is 3, and 3 commonly do mature, but the most usual number to mature is 2, and very often there is only 1. The emergence of only 1 parasite from a 1st-instar host often means that only 1 egg was laid, but equally often if the host is very small, it is due to the death of other individuals as young larvae. Except in very small 1st-instar hosts, however, premature death is uncommon, and even in such hosts at least one of the parasites always matures.

The number of eggs laid in late 1st-instar and early 2nd-instar larvae varies from 3 to 10, the mean being 7. The maximum number of parasites which can mature in hosts attacked at a time such that they die in the 2nd instar is 7.

In late 2nd and early 3rd-instar larvae, the number of eggs laid varies from 6 to 20, the mean being 12; and of these, the maximum number which can yield adult parasites is 15.

In 3rd-instar larvae, prepupae, and pupae, the number of eggs laid varies from 6 to 36, the mean being 17. The maximum number of parasites which can mature, however, is greatly in excess of the maximum number of eggs laid by a single individual in one host. The reason for this is that even the largest parasite individuals never lay more than 36 eggs at one time simply because they cannot do so. Dissections of large numbers of females in Java and Fiji showed that, except in small females, whose ovaries are reduced, each of the two ovaries contains 3 ovarioles and that the maximum number of mature eggs which one ovariole can contain at one time is 6. Each ovariole is a long tube with an enlargement at its proximal end. The mature eggs are stored side-by-side in the enlarged part. The immature eggs in the narrow distal part are arranged in a single chain, and even those that are most advanced in development and are situated at the proximal end of the narrow part are never completely developed. As soon as the mature eggs are discharged, they are replaced by others which mature in about 24 hours, but the maximum number available for discharge at one time is 6 per ovariole or 36 altogether. If oviposition is rendered impossible for a long time by the rarity or absence of hosts, 36 mature eggs may be laid in the first host which becomes

* These figures are based on dissections of 727 1st-instar larvae collected in the field at the beginning of October, 1933, at Nabavatu.

available, if it is a large larva or a pupa. But in all other circumstances, the number of eggs discharged into one large host by a large parasite is much less than the total number of mature eggs present at one time in the *parasite, and the usual number laid in a large larva or pupa is between* 15 and 20. If the number laid is between 15 and 20, the resulting parasites are all large and are uniform in both size and egg-capacity; * if it exceeds about 20, they are all undersized and are very variable in size and egg-capacity. Thus, the number of eggs normally laid is the number which results in uniformity in the resulting individuals.

The size of the egg is approximately constant, regardless of the size of the female, and therefore small females contain fewer mature eggs than *large ones. Females of medium size contain about 20 mature eggs, and* no more mature until these are laid. The 6 ovarioles are all approximately equal in size, in females of medium size, and the full complement is always present, the smaller capacity being due to uniformly smaller size in all the ovarioles. In small females, however, the maximum number of eggs which can mature at one time often does not exceed 12, and the ovarioles are reduced in number as well as size. There are often only 3 ovarioles (one ovary consisting of a single ovariole and the other of 2). Thus, it is *often impossible for small females to lay more than about 12 eggs in one* host, and females of medium size cannot lay more than about 20.

The maximum number of parasites which can mature in a large larva or a pupa is 68 for *P. nuciferae* and 56 for *P. reichei*. This can only happen in cases of superparasitism; and whenever the number of parasites which emerge from one host exceeds 36, and sometimes when it is 36 or less, superparasitism has occurred. Further reference to this phenomenon is made below. The minimum number of parasites which can mature in *large larvae or pupae is 5, except in special circumstances.* Unless the number of eggs laid exceeds 4 the parasites cannot devour the whole of the host contents and in these circumstances they die because they are prevented from breathing through the spiracles at the time when they require to do so. It occasionally happens, however, that the parasites, although too few to empty the host completely, are able to empty a part of it, usually the abdomen; when this happens, some or all of them mature.

i. *Superparasitism.*† This phenomenon occurs commonly when the parasites are excessively abundant and are about to suppress the host. *P. parvulus* can distinguish between living and dead larvae and pupae, and never oviposits in dead individuals, but it cannot distinguish between healthy larvae or pupae and those which are living but parasitised. Consequently, when the adult parasites are very abundant, living larvae and pupae of the pest containing both eggs and larvae of the parasite, or containing an excessive number of parasite individuals all in the same stage, are commonly to be found. In such cases, some of the parasites always mature, and the number of these is usually greater than the normal number for the stage of the host. The surplus parasites die as small larvae, their death being due to insufficient food, not to cannibalism. The

* *I.e.* the total number of eggs which they lay throughout their lives.

† The term "superparasitism" is here used to mean the excessive parasitism resulting from the attack of two or more adult parasites of the same species at different times on the same host individual.

larvae never attack one another. It is the youngest larvae, and the ones least suitably situated for obtaining food, which die. Since as many as 68 parasites can mature in large hosts, superparasitism in the latter does not result in many deaths, but in small larvae the death roll from this cause is sometimes heavy, the maximum number of parasites which can mature in smaller larvae being comparable to the number of eggs normally laid when superparasitism does not occur. The parasites which emerge from superparasitised hosts are always very small.

j. *The Duration of the Oviposition Period and the Frequency of Oviposition.* The female oviposits at irregular intervals almost throughout its life. There is always a short pre-oviposition period of not less than 24 hours from emergence from the mine. In females of large or medium size, oviposition usually commences on the day after emergence, but in small females (resulting from overcrowding and therefore under-nourishing) the eggs are very immature at emergence and there is usually a pre-oviposition period of 3 days. The post-oviposition period (between the laying of the last eggs and death) varies in duration from 3 to 5 days. On the average, the oviposition period may be regarded as being shorter by 4 days than the adult life.

The degree of regularity of oviposition depends upon the stage of the hosts available. If only small larvae are available, so that the number of eggs laid in each host is small, oviposition may take place nearly every day; but if only large larvae or pupae are available, so that the number of eggs laid on each occasion is large, oviposition occurs only a few times during the life of the parasite and at long intervals. In the latter case, the parasite usually oviposits abont 6 times altogether at irregular intervals, the average duration of which is about a week. It follows that when the available hosts are all small larvae the number of individuals destroyed by one parasite is very much greater than when all the hosts are large larvae or pupae.

Parasites that have no opportunity to oviposit for 4 or 5 weeks can still do so as soon as an opportunity arises. This is important in view of the conditions which prevail in one-stage outbreaks of *P. reichei.* In these circumstances, however, the total number of eggs ultimately laid is less than the normal egg-capacity, the production of eggs being diminished by delayed oviposition.

k. *Egg-Capacity.* The egg-capacity was determined in Java and in Fiji by two methods. First, records were kept of the numbers of larvae resulting from individuals kept separately in glass tubes and provided daily throughout their lives with fresh host individuals. The latter were dissected, and the contained parasites, if any, were counted 5 days after they were removed from the tubes. Keeping the host individuals for 5 days ensured that none of the parasites which they might contain should be so small as to be overlooked. The number of eggs in each female at death was ascertained by dissection. Secondly, females were kept alive in glass tubes for a month without being given any opportunity to oviposit, and were then dissected for examination of their ovaries, all the eggs, mature and immature, being counted. The results obtained by the two methods tallied satisfactorily, and it was therefore concluded that the second method was as sound as the first, and that the eggs present

after a month represent the total capacity. The first method, being very laborious, was applied to only 20 females (10 in each country), but the second, having been proved sound, was applied to 150 females.

It was found that the egg-capacity varies greatly with the size of the parasite, small individuals having smaller and fewer ovarioles. The females used in the experiments were therefore classified in 3 categories, small, medium, and large. Those classified as large were individuals which resulted from hosts in which the number of eggs laid was in no way abnormal; and since the parasite normally suits the number of eggs laid to the size of the host, these individuals must be regarded as representative of the species. Small and medium-sized females, however, are of common occurrence when superparasitism and excessive oviposition occur, and as these phenomena occur in Fiji in certain circumstances, it was important to ascertain whether they were economically detrimental.

The experiments showed that no females, however small or ill-nourished as larvae, are sterile, but that the smallest individuals have an egg-capacity of about 20 only. Actually, the capacity of the parasites in the "small" category proved to vary from 18 to 32. The capacity of the "medium" individuals varied from 35 to 67. "Large" females showed an egg-capacity varying from 60 to 85, the mean being 77, and this must be regarded as the egg-capacity of the species.

With only 2 exceptions, all the females for which complete oviposition records were kept, proved to have no immature eggs in their ovaries at death, and very few mature ones (0 to 6). There was every reason to suppose that they oviposited normally and to the normal extent, and it was evident that the number of eggs produced in the ovaries is approximately equal to the effective egg-capacity.

1. *Sex-Ratio.* The sex-ratio depends upon the predominant stage of the host, but females are always more numerous than males. Almost every host individual yields at least one male, but very many do not yield more than one.

The ratio was estimated by collecting large numbers of parasitised *P. reichei* individuals in the field and counting all the males and females which emerged from them. Two collections were made, the first consisting solely of 336 1st-instar larvae and the second of 617 3rd-instar larvae and pupae. The 1st-instar larvae yielded 628 *P. parvulus* (the mean being about 2 parasites per host) and of these, 392 were females and 236 males. For 1st-instar hosts, therefore, the ratio is :—♀ : ♂ = 1·66 : 1·00. The 3rd-instar larvae and pupae yielded 9,265 parasites (the mean being 15 per host) and of these, 7,531 were females and 1,734 males. Thus for large hosts, the ratio is :—♀ : ♂ = 4·34 : 1·00, and the males are only 18·7% of the total. (In Java, for a much smaller number of parasites reared from large larvae and pupae of *P. nuciferae* and *G. xanthomelana*, the ratio was :—♀ : ♂ = 4·51 : 1·00.) The majority of large hosts yield about 17 parasites which usually include 3 or 4 males, but many yield fewer parasites and only one male.

In Java, where all stages of the various hosts are always present simultaneously, and in Fiji in multiple-stage conditions, the sex-ratio is approximately :—♀ : ♂ = 3·5 : 1. On account of the tendency to collect a larger proportion of large mines than small ones in the field when all

stages are present, any estimate of the sex-ratio in multiple-stage conditions must be regarded as approximate only.

The emergence of a higher percentage of males from small mines than from large ones appears to be attributable to ability on the part of the female to control fecundation of the eggs. This question is further discussed in a later Section.

## E. The Effect of Parasitism upon the Host.

The attack of the adult parasite has no immediate effect upon the host except that the latter usually feels the withdrawal of the ovipositor and moves along the mine. The host continues to develop normally for several days, but eventually it becomes lethargic and then dies as a result of the activities of the parasite larvae within it.

The extent of the development of the host after the initial attack of the parasite depends upon the species of host. *P. nuciferae* develops much more rapidly than *P. reichei,* and if larvae of these two species are initially attacked in the same developmental stage, those of *P. nuciferae* develop much further before they are killed than those of *P. reichei.*

The 1st and 2nd-instar larvae of *P. nuciferae* invariably undergo one moult, though never more than one, before they are killed, even if they are attacked at the very beginning of either instar. The moult occurs at the usual time. Larvae of *P. reichei,* on the other hand, if attacked within the first half of the 1st or 2nd instar, attain full growth for the instar in question but are invariably killed before they can moult and they therefore die in the instar in which they have been attacked. *P. reichei* larvae attacked in the second half of the 1st or 2nd instar, however, moult once, at the normal time, before they are killed. Larvae, of either species, attacked in the second half of either of these two instars, resume feeding at the usual time after the moult, but whereas, after resumption of feeding, those of *P. nuciferae* attain almost the full growth for the new instar those of *P. reichei* die at an early stage in that instar.

Parasitised larvae which undergo a moult before they are killed are always smaller after the moult than healthy larvae in the same stage of development. The difference is most noticeable in the chitinised plates of the prothoracic segment, except in the case of larvae attacked shortly before moulting.

Larvae attacked early in the 3rd instar do not pupate; those of *P. nuciferae* die as prepupae, and those of *P. reichei* as full-grown larvae. If the host is a prepupa, or if it is nearly full grown and is due to feed for only one more day, when the adult parasite oviposits in it, it pupates before it is killed; but if the attack is made more than one day before cessation of feeding, the host dies as a prepupa. This applies to both species.

The period which elapses between the initial attack of the parasite and the killing of the host by the resulting larvae within it varies with the stage of the host and with temperature. In individuals attacked as full-grown larvae, prepupae, or pupae, in the hot season, death occurs, on the average, 6 days after the initial attack. This applies to both *P. nuciferae* and *P. reichei.* In the cool season in Fiji, the corresponding mean period was 7 days. The variation in this period is slight (5–6½ days in hot weather,

6½–7½ days in cool weather). For all younger individuals, the period is longer and much more variable. Larvae attacked in the early part of the 3rd instar die, in hot weather 7, 8, or 9 days later. In parasitised 1st and 2nd-instar larvae, the rate of growth of the contained parasites varies very greatly, and the period which precedes death varies correspondingly. For both host species and both instars, the period in the hot season is 10 to 20 days, the mean being 13 days; and in the cool season in Fiji the period was found to vary from 10 to 22 days, the mean being 16 days. In the case of *P. reichei*, it was found that moulting causes delay in the development of the parasites, and consequently larvae which moult after being attacked live rather longer, in general, than those which do not. This does not apply to *P. nuciferae* because the instars are so much shorter that all parasitised larvae moult once.

Parasitised larvae feed normally until about 18 hours before they are killed, except when they cease feeding earlier to moult. The final onslaught of the contained parasites upon the vital organs is very sudden, and the lethargy which is the first result of it lasts for only a short time. A few hours before it is caused to cease its normal activities the host acquires an abnormal colour, becoming very pale and often almost white. This paleness is maintained almost throughout the brief period of lethargy, but just before death occurs dark brown blotches and spots begin to appear on the surface and these rapidly increase in extent, number, and depth of colour until, 24 hours after death, the larva is uniformly black or dark brown all over its surface (Plate XXIII). When death occurs, a drop of fluid excrement, to which we have already referred, is expelled from the anus of the host, and this rapidly dries and usually attaches the host firmly to the wall of the mine by its posterior extremity. About 36 hours after death, air spaces first appear inside the skin amongst the parasite larvae, which are now full grown, but these are not readily visible on account of the dark pigmentation of the host skin. Until this time the host skin remains normally soft, but it now begins to dry, no longer having liquid contents, and it dries distended and in its normal shape, except for bulges here and there caused by the tightly-packed parasites within. The skin does not dry completely, however, until about 5 days after death. When it is dry, it is hard, very brittle, and almost black. It is nearly opaque, but if a bright light is shone through it the contained parasites can usually be seen dimly.

These changes in the external appearance of parasitised larvae, and the appearance of the parasite pupae as seen through the host skin, are illustrated in Plate XXIII. Similar changes take place in pupae, but on account of the chitinisation of the pupal integument, the changes are less marked and the final colour is dark brown, not black. The distention and extension of the abdominal segments of the pupa, however, are very marked.

The commencement of the period of lethargy, in both larvae and pupae, corresponds with the beginning of the 4th instar of the contained parasites. The death of the host occurs just before the parasites attain maximum growth, and the appearance of air spaces marks the attainment of maximum growth. The pupation of the parasites occurs about 2 days before the host skin becomes completely dry and brittle.

The parasite larvae are often visible through the host skin when they are quite small, sometimes several days before the host dies.

## F. Life Cycle.

The rate of development varies with temperature and with the stage of development of the host. In large larvae and pupae the rate is nearly constant at a given mean temperature, but in small larvae it varies very greatly, and is usually much slower than in large larvae or pupae in spite of the fact that the number of eggs laid is suited to the size of the host. In view of this latter circumstance, it appears that the difference in rate of development in hosts of different sizes is due to changes in the quality of the food, rather than the quantity, with growth. All the parasites in one host individual develop at almost the same rate, except in cases of superparasitism or excessive oviposition.

At a daily mean temperature of 85° F. (absolute maximum 92° F., absolute minimum 79° F.) in the room in which the observations were made, the life cycle of *P. parvulus* in large larvae and pupae of *P. reichei* proved to be as follows :—*

| | |
|---|---|
| Incubation Period . . . . . . | $2\frac{3}{4}$ days (constant) |
| 1st Instar ,, $1\frac{1}{2}$ days (mean) | |
| 2nd ,, ,, 1 day ,, | |
| 3rd ,, ,, 1 ,, ,, | |
| 4th ,, ,, (to excretion) $3\frac{1}{2}$ days ,, | |
| Prepupal Period 1 day (constant) | |
| Total Larval Period . . . . . | $7\frac{1}{4}$–$9\frac{1}{2}$ days; mean, $8\frac{1}{4}$ days |
| Pupal Period (to *emergence from pupa, not* from mine) . . . . . . . | 9 days (constant) |
| Total Period (oviposition to emergence from pupa) . . . . . . . | 19–21 days; mean $19\frac{1}{2}$ days |

(The figures are correct to the nearest quarter of a day.)

In Java, at slightly higher temperatures, the corresponding figures for the total period for individuals in large larvae and pupae of *P. nuciferae* were 17–21 days, mean $18\frac{1}{2}$ days (20 host individuals). The slightly more rapid development is attributable to the temperature, not to the species of host.

In the cool season in Fiji, at a daily mean temperature of 78° F. (absolute maximum 87° F., absolute minimum 70° F.), the total period for large hosts covered 20–24 days (48 host individuals), the mean being 22 days. The difference in the period of the life cycle in the hot and the cool seasons was thus comparatively small, and proved much less in proportion than that of *P. reichei* itself.

For small hosts (1st and 2nd instar) the total period of the life cycle, from oviposition to emergence from the pupae, was very much longer in nearly all cases, both in the field and in the laboratory. In the cool season in Fiji, it varied from 22 to 38 days for 1st-instar hosts, and 22 to

* **For method employed, see Section IX.**

35 days for 2nd-instar hosts, the mean in the first case being 29 days and in the second 26 days. The lengthening occurred in the larval period only, the incubation and pupal periods varying only with temperature, not with the size of the host. Further, dissections on different days of many larvae parasitised on the same day showed that the lengthening occurred in the 2nd and 3rd instars of the parasites, the 1st and 4th instars being nearly constant in duration.

## G. *P. parvulus* as a Parasite of Pupae in an advanced Stage of Development.

Every individual of each host species is liable to be attacked from the time when it escapes from the egg until it emerges as an adult from the pupa. Pupae which are about to produce adults, however, are unsuitable as food for the parasites, the latter usually dying of starvation as larvae because the body-fluid of the adult beetle is insufficient in quantity for their requirements. The female parasite never attempts to oviposit in adult beetles which are resting in the mines prior to escaping, but it is unable to discriminate between pupae which are about to yield adults and those which are in an earlier stage of development. Sometimes, therefore, *P. parvulus* oviposits in pupae which are unsuitable as hosts for its progeny.

Experiments were made to ascertain precisely at what stage in its development the pupa becomes unsuitable for the development of *P. parvulus*. In pupae of *P. nuciferae* and of *P. reichei*, the stage of development reached by the adult is apparent from certain colour changes. Thus, 5 days before the adult is due to emerge, the eyes become almost black; and then, 2 days later, the mandibles become black with comparative suddenness. Other similar changes follow. Experiments showed that so long as the stage of development is such that the eyes only are dark in colour, the attack of *P. parvulus* is followed by normal development of the resulting parasites; but if the host, when first attacked, has reached the stage when the mandibles as well as the eyes are dark, the resulting parasites sometimes mature and sometimes die; and if the host has passed, by more than 12 hours, the stage when the mandibles become dark, the parasites always fail to mature and die as larvae. The critical stage in the development of the host, therefore, is marked by the darkening of the mandibles, and this occurs 3 days before the adult beetle is due to emerge. The host dies in any case, but if attacked within 2½ days of the time when it is due to emerge as an adult from the pupal skin, emergence takes place normally and the individual dies as an adult in the mine.

The attack of the parasite at the time when the mandibles first become black almost invariably results in the death of the host individual while still within the pupal skin, but as a completely developed adult. This is curious, since the eggs of the parasite do not hatch until nearly 3 days after they are laid, and host larvae and pupae are not normally killed until the parasites reach the 4th instar. It is not to be supposed that the parasite larvae, when newly hatched, attack the vital organs or feed on anything but the body-fluid; and the death of the host after 3 days must

therefore be attributed either to the commencement of absorption of the body-fluid by the very young larvae or else to injury caused by the adult parasite when ovipositing, although neither of these operations ever affects younger host individuals. Very occasionally, however, a parasitised individual attacked at the critical time emerges in due course from the pupal skin and dies soon afterwards in the mine, and still more rarely, the parasites succeed in maturing in an adult beetle which has so emerged, and in escaping from it in the ordinary way. This latter event was observed in the field as well as in the laboratory. *P. parvulus*, therefore, may emerge from larvae, pupae, or adults, although it oviposits in larvae and pupae only, but in general its development is limited to host individuals attacked at or before the stage when the mandibles of the adult are apparent in the pupa.

### H. Multiparasitism in which *P. parvulus* is Involved.

In Java, *P. painei* and *D. javanica* occasionally attack individuals of *P. nuciferae* which have already been attacked by *P. parvulus*, and the latter occasionally attacks pupae already parasitised and paralysed by *P. painei*. In Fiji, *E. hispidarum* attacks *P. reichei* individuals already parasitised by *P. parvulus*.

Multiparasitism involving *P. parvulus* and either *D. javanica* or *E. hispidarum* results in the death of the internal parasite in all circumstances except when the latter attacks the host 5 or more days before the external parasite attacks it. The external parasite can mature on hosts which it attacks at any earlier time, relative to the attack of *P. parvulus*. The 2 external parasites are liable to oviposit, in a mine in which the Hispid larva is already parasitised by *P. parvulus*, at any time until the internal parasite larvae are full grown, and *P. parvulus* is liable to attack a Hispid larva paralysed by either of the external parasites at any time before the eggs of the latter hatch. We have already had occasion to refer to the detrimental effect upon *P. parvulus* of competition with *D. javanica*, and this is due to the fact that *P. parvulus* requires to lead by 5 days if it is to survive, while the external parasite can survive in all other circumstances.

Multiparasitism involving the 2 internal parasites, *P. parvulus* and *P. painei*, was caused to occur in the laboratory at Buitenzorg without difficulty. It was observed only once in the field, however, and in this instance the host was a pupa of *G. xanthomelana* from which adults of both sexes of both parasites emerged. Laboratory experiments showed that if a host pupa is attacked by both species at the same time, *P. painei* develops and *P. parvulus* dies; that when one species attacks the host 2 days or more before the other, only the one which makes the attack first survives; and that when *P. parvulus* attacks the host 1 day before *P. painei*, both species survive, although in small numbers only. On the whole, therefore, *P. painei* has the advantage. The point of special interest, however, is that the condition of paralysis, followed rapidly by death, which is caused by the attack of *P. painei* is not in itself detrimental to *P. parvulus* although the latter normally develops in living hosts. Similarly, the paralysis of the host individuals by *D. javanica* and *E. hispidarum* is not detrimental to *P. parvulus*. Host individuals killed by

*P. painei* proved to be liable to be attacked by adult *P. parvulus* until their contents are completely devoured.

Multiparasitism is necessarily a very rare occurrence in the field except at those times when the parasites are about to suppress the pest, and even on these occasions it cannot result in the elimination of *P. parvulus*. In Java, no matter how abundant *D. javanica* may be, or how thoroughly it eliminates *P. parvulus* as a larval parasite, the latter can always survive because it attacks pupae as well as larvae and because it has hosts in plants other than coconuts; and *P. painei* does not compete appreciably in coconuts because it does not frequent them extensively, and it cannot suppress *P. parvulus* appreciably in bananas because it only attacks pupae, which are always much less plentiful than larvae. In Fiji, *P. parvulus* is likely to suffer, in multiple-stage outbreaks only, by competition with *E. hispidarum* (though no opportunity has yet arisen to test this point), but its complete elimination is impossible because it attacks pupae as well as larvae.

## I. Host Selection

In the course of bulk-breeding work with *P. parvulus* in Java, it was repeatedly observed that some females from banana mines showed a strong predilection for banana mines when ovipositing, that some females from coconut mines showed the same predilection for coconut mines, and that other females, from either plant, attacked mines in both coconuts and bananas equally readily. It was further observed that the preferences and the lack of preference were hereditary for at least 3 generations (the observations were not carried further). It was concluded that in any locality in which both coconuts and bananas are plentiful there are 3 strains of *P. parvulus*, one frequenting bananas and therefore attacking *G. xanthomelana*, one frequenting coconuts and therefore attacking *P. nuciferae*, and one frequenting coconuts and bananas equally. This condition in *P. parvulus* would appear to represent the beginning of the formation of distinct biological races.

Every parasite individual that showed a marked preference for mines in one of these two plants, invariably could, in the course of time, be induced to attack mines in the other plant species, and the resulting offspring were always normal in development, sex-ratio, and every other respect. Further, cross-pairing between any two strains always took place as readily as pairing within one strain, and always resulted in offspring which were normal in every respect and which reproduced normally, generation after generation; and no morphological differences in the 3 strains could ever be detected. It cannot be said, therefore, that distinct biological races already exist, but there is clearly a tendency in this direction.

The most convincing of many instances of the existence of these different strains was that which resulted from 2 parasitised pupae of *G. xanthomelana* which were found in leaves of the same banana plant. The parasites which emerged (on different days) from these 2 pupae were almost identical in size, sex-ratio, and number. Both batches, when 3 days old, were provided with pupal mines of *P. nuciferae* in coconut, but,

whereas all the females of one batch oviposited almost immediately, none of those in the other batch oviposited at all or showed any attraction for the mines, which were left in the tubes with them for 3 days. When the coconut mines were removed from the tubes containing the parasites which had not oviposited, banana mines were inserted, and these were immediately attacked by almost all of the parasites. After 14 more days, during which they were given no mines, the parasites which had previously attacked banana mines only were provided with coconut mines again, and this time some of them oviposited, though not with the normal readiness. The offspring which resulted from these coconut mines attacked mines in coconut more readily than those in banana.

These and many other similar observations led to two conclusions. First, any individual of *P. parvulus* with an inherent tendency to frequent one plant species will, if unable to find hosts in the latter after a considerable time, forsake it and seek hosts in other plant species which are frequented by other individuals of its own kind; and secondly, the *species P. parvulus, as an entity, frequents both bananas and coconuts* equally.

J. Artificial Host-Selection and the Production of Males.

Although its hosts in the field are mining Hispids only, *P. parvulus can, in certain artificial conditions, be induced to attack non-mining* species. Thus, in Java, it attacked pupae of *Plesispa reichei* very readily if these were inserted into mines of *Promecotheca* from which the normal occupants had been removed, although it was not in the least attracted by them in any other circumstances. The parasite larvae fed normally in the abnormal host individuals and developed at the usual rate, but when they emerged they proved to be all males, without exception (6 *Plesispa* pupae, and an average of 13 *P. parvulus* per pupa). This was remarkable, since it was certain that the parent parasites had paired, and in all normal circumstances nearly all the parasites from one host are invariably females. It was therefore certain that the abnormal nature of the host was in some way connected with the productiou of the entirely male batches of parasites.

When the *Plesispa* individuals were removed from the tubes containing the parasites, mines containing pupae of *P. nuciferae* were inserted. These pupae were parasitised in due course, by the parasites which had already attacked *Plesispa*. They were expected to yield *P. parvulus* individuals which were normal in every respect, but the parasites which emerged were actually very abnormal in tbat 3 of the 6 batches were entirely female (the numbers of parasites which emerged being 17, 19, and 21). The other 3 were normal. It is an almost invariable rule that there is at least one male in every batch, and there can be little doubt that the peculiar results obtained were due to the earlier production of wholly male batches by the same parent parasites. If this is true, the only possible explanation of the results of the first experiment is that the parent females, although impregnated, were induced, by the presence of pupae of an unusual nature in usual mines, to lay unfecundated eggs. Unfortunately, no opportunity for further investigation of this question arose, and the explanation of the phenomenon must remain in doubt.

It is interesting, in this connection, to recall that in certain parasite species, individuals resulting from small hosts are usually males and those from large hosts are usually females. *D. javanica*, *E. hispidarum*, and *P. parvulus* are similar cases, in that males result far more commonly relatively, from small hosts than from large ones. Another similar instance is provided by certain parasite species which are both primary and secondary, and produce females when they are primary and males when they are secondary, the hosts in the latter case being much smaller. The most interesting case of all is that of certain species which attack scale insects, and which are typical primary parasites but occasionally oviposit, apparently by accident only, in a parasite individual which is present in the attacked scale insect. The adult parasite which results from the egg laid by accident in the primary parasite already present, instead of in a healthy scale insect, is a male. Many other instances of the production of males in special circumstances witb regard to the host could be cited, but the examples which we have considered suffice to show that in some cases the parent female is able to control the fecundation of the eggs as it lays them and in others the limited quantity or unusual quality of the food of the larvae causes them to become male by a process in the nature of castration.

In the case of *P. parvulus*, however, the available evidence seems to indicate that the production of males is directly due in all cases to the parent female, not to any influence upon the offspring as larvae. The fact that large hosts, in which many eggs are laid, yield only a small proportion of males, and small hosts, in which few eggs are laid, yield a much higher proportionof males,can be explainedeither onthe assumption that the first few eggs laid in every host are usually and automatically unfecundated, the females being uninfluenced by the size of the host except as regards the number of eggs laid; or upon the assumption that the female, when ovipositing, controls the fecnndation of the eggs, as well as the number laid, in response to the size or other character of the host. This applies to *D. javanica* and *E. hispidarum* also. The emergence of entirely male batches of *P. parvulus* from the *Plesispa* pupae, however, can only be explained on the second of these assumptions, and it is reasonable to assume further that in all circumstances the female, when ovipositing, controls fecundation in response to stimuli from the host, though this cannot be regarded as proved. The special suitability of these Hispid parasites for more detailed investigations on these lines is worthy of comment.

## VIII. THE INTRODUCTION INTO FIJI OF PARASITES FROM JAVA, AND THE CONSEQUENT CONTROL OF *P. REICHEI*.

### A. Shipment from Java, Arrival in Fiji, and initial Plans for Breeding *P. parvulus*.

The preparations for the shipment of parasites to Fiji were made at the Instituut voor Plantenziekten, Buitenzorg. Six large wooden cages (6 ft. × 3 ft. × 3 ft.), with wire-gauze sides and front, were constructed, and in these *P. nuciferae* was bred in large numbers, the necessary seedling coconut palms being planted in tins and inserted into the cages as required. It was arranged that 24 palms (4 per cage) should be heavily stocked with mines and eggs on the date of sailing from Java, so that all stages of *P. nuciferae* should be available for breeding the parasites during the voyage. In addition to the cages, a large wooden box of the size of a cabin trunk was also constructed, and this contained 2 movable trays, one above the other, with a considerable space below the lower one, for holding the glass tubes and other apparatus required for breeding the parasites.

The consignment was loaded on to lorries and taken to Tandjong Priok (the port of Batavia) in the early morning of April 17th, 1933, which was the date of sailing. The vessel employed was the S.S. *Van Rees* of the K.P.M. line, which was running between Singapore and Sydney, via Java, New Guinea, New Hebrides, and New Caledonia ports. This vessel arrived at Noumea, New Caledonia, on May 10th, and at Noumea the consignment was transhipped to the S.S. *Karetu*, which reached Fiji on May 14th. Before arrival at Noumea, all the cages were emptied, the palms, soil, and tins being thrown overboard to prevent the introduction into New Caledonia or Fiji of any undesirable organisms. By this time no more mines of *P. nuciferae* were required, and actually the number of palms shipped from Java proved unnecessarily large, having been planned to guard against emergencies which did not arise. The consignment, on arrival in Fiji, consisted of adult parasites and of parasitised larvae and pupae of *P. nuciferae*, all contained in 4 in. × 1 in. glass tubes.

Owing to the rarity of *P. reichei* at the time in the neighbourhood of Suva, the capital, and on most islands except those of the Lau Group, it was necessary to transport the parasites as soon as possible to Lau, where many severe outbreaks of *P. reichei* were then raging, and to make one of the Lau islands a centre of operations for breeding and distributing the parasites. Nabavatu, on the island Vanua Balavu, was adopted as headquarters for the work, at the invitation of Mr. K. J. Allardyce, the owner of the property, whose hospitality and help were invaluable at this time and for the next 11 months.

The parasites were taken by motor launch from Suva to Nabavatu, and arrived at their destination on 24th May, the whole voyage from Java

having covered 37 days. *P. parvulus* arrived in excellent condition. 1.200 individuals of this species were landed at Nabavatu, and these consisted of 900 pupae in pupae of *P. nuciferae*, which had been parasitised on board ship before arrival at Noumea; and 300 adults, of which a few had survived the whole voyage, having been shipped as adults in Java, and the remainder had been reared *en route*. A strong colony of *D. javanica* was also landed, and this consisted of 378 adults, all of which had been reared from eggs laid during the voyage. *P. painei*, however, was landed in poor condition, having completely failed to oviposit during the voyage, although it bred satisfactorily in Java and the same methods were employed at sea. The reasons for its failure to breed at sea were never discovered. Only 14 living individuals (3 males and 11 females) were landed at Nabavatu, and these had emerged early in the voyage from host individuals parasitised in Java. The failure of *P. painei* was, however, partly due to the fact that no very careful attention had been paid to methods of breeding it in bulk before shipment was attempted, the available time having been devoted principally to *P. parvulus*.

On account of the successful breeding of *P. parvulus* en route, and the consequently plentiful supply on arrival of individuals which had not yet become adult, there was ample time, after arrival at Nabavatu, to make a general survey of the outbreak area there before breeding operations were commenced. This survey was an essential preliminary, because the outbreak was of the one-stage type and the necessity therefore arose for ascertaining whether the stages required for the parasites were available, and if not, how soon they would become available. It was found that the dominant stage of the pest at the end of May was eggs. Beetles were abundant, and a very few belated pupae were fonnd, but larvae were entirely absent. It was therefore decided to liberate the few old adults of *P. parvulus* immediately, in the belief that they would sncceed in finding a few of the belated pupae and that some of them would live until the eggs of the pest began to hatch; and to use the few pupae which were found for ascertaining whether *P. parvulus* would attack and mature in *P. reichei*, in accordance with expectations, and for increasing the stock of *P. parvulus* sufficiently, if the species proved to breed satisfactorily, to ensure its survival in reasonable numbers until suitable *P. reichei* larvae should become available in abundance for the commencement of bulk breeding.

*P. parvulus* at once attacked the local species of *Promecotheca* with great avidity, and its progeny matured normally in due course. On 2nd June, other localities on the island were visited for the purpose of supplementing the supply of suitable *P. reichei* individuals, and this was satisfactorily accomplished. Many other outbreaks, some already severe and some developing, were noted, and it was evident that by the end of the year the infestation, unless checked, would be very severe all over the island. It was found that in all the outbreaks the predominant stage of the pest was nearly the same as at Nabavatu.

Since there are no regular inter-island communications in the Lau group and the bulk-breeding of *P. parvulus* required an abundant daily supply of larvae or pupae of *P. reichei*, there was no possibility of obtaining the necessary material from any source other than Nabavatu itself or

neighbouring localities on the same island. *P. parvulus* can be bred in large numbers, only by the use of large larvae or pupae as hosts. It attacks small larvae equally readily, but the use of small larvae involves the adoption of elaborate and tedious methods which, together with the fact that small larvae yield only 2 or 3 parasites, make bulk-breeding with small larvae impossible. It was therefore evident at the outset that the correct plan of procedure would be to devote the period of predominance of large larvae and pupae, which recurs every 3½ months, to bulk-breeding and distribution of the parasites, and to devote the intervening periods to maintaining a small but sufficient stock of parasites and to the careful study of the multiplication and spreading of the species in the field. This latter investigation was regarded as a most important part of the work, and was carried out thoroughly from the commencement of operations. It was anticipated, from a knowledge of the reproductive capacities of host and parasite, that unless any detrimental factor had been overlooked, the complete suppression of the pest throughout Fiji could be accomplished within a year, and that after 6 months, the parasites would be sufficiently numerous in the localities in which they were first liberated to render further laboratory breeding unnecessary and to suppress the pest in those localities. For these reasons an effort was made from the first to establish the species as soon as possible at Nabavatu, in the hope that bulk-breeding would not be necessary for more than one period of predominance of large larvae and pupae, and to this end other islands and localities were neglected for the first three months. It is interesting to record, as an instance of the precision with which *P. parvulus* behaved, that the theoretical estimation of the time required by the parasite to suppress the pest, which was submitted in a report to the Director of Agriculture at the commencement of operations, proved almost exactly correct.

The breeding of *P. reichei* in captivity is very much more difficult than that of *P. nuciferae*, on account of the differences to which we have already referred. Although possible on a small scale, it was out of the question as a means of obtaining the very large quantity of mines necessary for breeding *P. parvulus*. Collection of mines in the field was therefore the only means of carrying out the work, and the utilisation to the full of the first period of predominance of large host individuals was of great importance if the work was to be accomplished with despatch.

### B. The Breeding and Liberation of *P. parvulus*.*

*P. parvulus* was bred continuously in the laboratory at Nabavatu for 6 months, from the end of May until November. In November it became so plentiful in the field that no further continuous breeding was necessary. Bulk-breeding was commenced at the beginning of August, when 3rd-instar larvae first became available, and was continued throughout August and September, first with larvae as hosts and then with pupae. Only this one period of bulk-breeding proved to be necessary, as when large larvae and pupae next became available (December and January) the parasites could be obtained in countless thousands in the field. The

* The method adopted for bulk-breeding was the same as that used for shipment, and is described in Section IX.

number of parasites reared from eggs in the laboratory was 7,648. With the exception of a few which were retained from time to time for breeding, all these were liberated on various islands in Lau. The number of parasites reared from pupae collected in the field in their hosts was approximately 18,000, and of these, some were liberated in Lau and some in other parts of Fiji. The first liberations were made on 26th May, 1933, and the last on 30th April, 1934. The total number of parasites liberated was about 26,000, and these consisted of 48 different colonies. The number per colony varied from 100 to 1,400, the mean being approximately 500. Actually, the numbers liberated proved unnecessarily large, as regards both the number of colonies and the number of parasites per colony, and the final conclusion was that 2,000 individuals would have sufficed to have established the species throughout the whole of Fiji and that the suppression of the pest would have taken only 3 months longer than it actually took if only 2,000 had been liberated. This, however, could not be foreseen.

For every colony liberated a record was kept of the number of males and females in the colony, their age in days, and the degree of abundance and predominant stage (if any) of the pest in the locality in question. It was subsequently found, however, that in all cases the parasites became established, and it was concluded that, within reason, all these factors were immaterial. Parasites 35 days old served to establish the species as satisfactorily as those which were only 1 day old. If the parasites were liberated at a time when only adult beetles were present, some of them survived long enough, even if 35 days old when liberated, to attack the first larvae which appeared. So long as the pest was present, the parasites could become established, the degree of abundance of the pest being immaterial. Further, although on several islands the parasites were liberated in several different and widely separated localities, those in each locality constituting one colony, it was found that the capacity of the species for spreading was so great that there was very little advantage in liberating more than one colony on each island. For these reasons, it is considered unnecessary here to give full particulars for every colony, and in the following table only the total number of parasites and colonies for each island is shown, and the data concerning the ages of the parasites and the state of the pest at the time are omitted.

Since the sea is the highway of Fiji, the distribution of *P. parvulus* to different parts of the Colony involved lengthy voyages, often in rough weather, and necessitated the chartering of a seaworthy vessel, there being no regular shipping services to most of the islands, especially in Lau. The vessel principally employed was a two-masted sailing-ship with an auxiliary engine. The chartering of such a vessel is an expensive procedure, and it was therefore necessary to carry out the work as quickly as possible, travelling at sea by night whenever this was practicable. Moreover, since a few long charters are much cheaper than several short ones, it was necessary to ship as many parasites as possible at one time so that many different islands could be dealt with during one voyage. This involved planning the work of rearing the parasites at Nabavatu in such a way that at least 10,000 adults would be available for shipping on the day when the vessel was due, allowance being made, in the absence of all means

*Table XI. Liberation of* P. parvulus *in Fiji.*

| Island. | No. of Colonies. | Date or Period of Liberation. | Total No. of Parasites Liberated. |
|---|---|---|---|
| Vanua Balavu . . . | 24 | 26th May, '33, to 11th Jan., '34 | 11,700 |
| Kanacea . . . . | 3 | 25th Aug. and 28th Dec., '33 | 1,400 |
| Munia . . . . | 2 | 16th Sept., '33 | 1,700 |
| Mago . . . . | 2 | 13th Dec., '33 | 900 |
| Cicia . . . . . | 2 | 14th Dec., '33 | 900 |
| Lakeba . . . . | 2 | 16th Dec., '33 | 1,100 |
| Naiau . . . . | 1 | 17th Dec., '33 | 700 |
| Taveuni . . . . | 4 | 29th Dec., '33, and 23rd Jan., '34 | 1,900 |
| Laucalla . . . . | 1 | 24th Jan., '34 | 600 |
| Rabi . . . . . | 1 | 25th Jan., '34 | 800 |
| Vanua Levu* . . . | 3 | 26th Jan., '34 | 1,800 |
| Naitauba . . . . | 1 | 19th April, '34 | 500 |
| Ovalau . . . . | 1 | 21st April, '34 | 1,400 |
| Viti Levu †. . . . | 1 | 30th April, '34 | 500 |
| Totals . . . . | 48 | | 25,900 |

* Udu and Labasa.
† In forest, nr. Suva, for *P. bicolor.*

of communication, for the probability that the vessel, booked several weeks ahead, would be late. Apart from short trips to islands near to Nabavatu, such as Kanacea and Munia, which were reached by launch in a few hours, the whole of the work of distributing the parasites was accomplished in two charters, one of 6 days, during which Kanacea, Mago, Cicia, Lakeba, and Naiau were visited, and one of 12 days, during which Taveuni, Laucalla, Rabi, Vanua Levu, Yacata, and Kanacea were visited. Parasites were taken to Naitauba and Ovalau in the course of the return trip to Suva at the end of the campaign.

For all these voyages the parasites were shipped in the large wooden box coustructed in Java, the top tray of which contained 90 glass tubes (4 in. × 1 in.) arranged side-by-side in 3 rows. About 70 adult *P. parvulus* were inserted into each tube, and the tray, when full at the beginning of a voyage, contained about 7,000 parasites. Each tube contained about 10 males, and it was found that this ensured the impregnation of all the females. In order to ensure a sufficient supply of males, a few parthenogenetic broods were reared every week during the breeding operations, the females to be used for this purpose being captured as soon as they emerged from their hosts, so that pairing could not take place. During each voyage, the parasites were provided, by a native assistant, with fresh drops of honey for food whenever necessary, and a microscope was carried and used on board for necessary routine operations.

The actual freeing of the parasites was a very simple matter. The cotton-wool bungs were pulled out of the tubes, and the open ends of the tubes jerked against the trunks of the coconut trees. The parasites,

which proved resistant to most forms of rough handling, shot out of the tubes on to the trunks of the trees, and if the weather was sunny, most of them at once flew up to the leaves and began searching for mines. If the weather was dull, many of them remained on the trunks until the next morning, but this was immaterial.

## C. The Multiplication and Spreading of *P. parvulus* in Fiji.

### 1. Multiplication and Spreading within a Single Outbreak Area.

The progress of *P. parvulus* in the field was studied continuously at Nabavatu from 26th May, 1933, when the first colony was liberated, until the middle of April, 1934, when the work was regarded as finished. This estate was particularly well suited for this part of the work, because it consists of many comparatively small areas separated from one another, partly or completely, by rocky hills, belts and patches of forest, and deep bays. The estate as a whole served very well for the study of the effect of natural barriers upon the spread of the parasite, and the continuous coconut areas were large enough for the investigation of its spread in the absence of barriers. Further, the complete isolation of the estate from all other coconut areas on the island prevented the immigration of the pest or parasites from other localities and so prevented confusion in the interpretation of the observations made.

Nabavatu is situated towards the north-west end of the island Vanua Balavu. It is bounded by very steep, rocky, slopes and cliffs, and the whole of it is extremely rugged and rocky. The soil varies greatly in depth, but the average depth does not exceed 2 ft., and the limestone rock, of which the whole of the north-western end of the island consists, projects through the soil in great spikes and boulders. Despite the comparative lack of soil and the excessively porous nature of the rock, the whole of this part of the island, except those areas which have been cleared for coconuts, is densely forested. The steep slopes drop straight down to the sea, so that there are no coastal flats and, except in a few small inlets, no beaches. The lack on this part of the island of the usual coastal fringe of coconuts results in the complete isolation of the coconut areas of Nabavatu Estate, which is bounded by the sea on both sides and by wide stretches of virgin forest, devoid of coconuts, at the two ends.

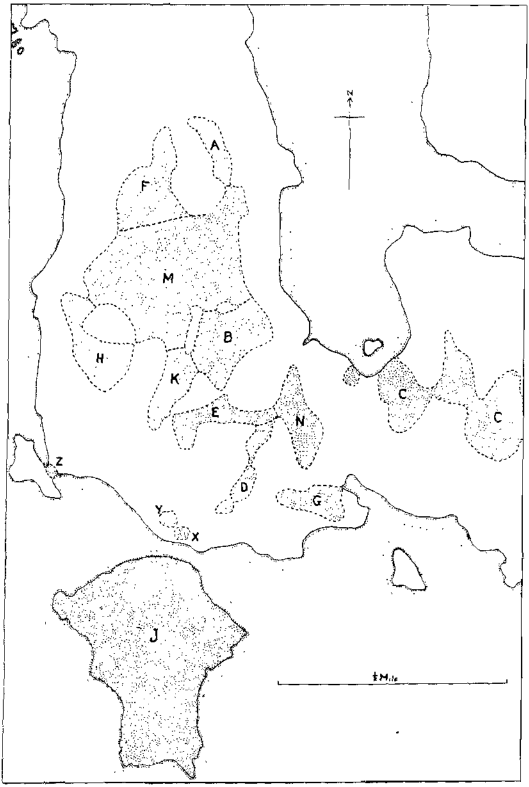
In 1929, an extremely severe one-stage outbreak of *P. reichei* occurred at Nabavatu and covered the whole estate, maximum defoliation prevailing everywhere. Similar outbreaks occurred at the same time on many other Lau islands. During the wet season of 1929–30, and during 1930, the outbreak at Nabavatu was terminated by the indigenous parasites, the pest being at their mercy since it could not spread further. The trees then began to recover, and by 1933 they had completely recovered in most areas. In the meantime, however, at the end of 1931, the pest again began to increase in one-stage form in certain areas, and maximum defoliation was reached in these areas at the end of 1932. Spreading then took place in the usual way, and by May, 1933, when *P. parvulus* was first introduced, it was evident that another extremely severe outbreak was in progress and that the whole estate would again be infested by the beginning of 1934 unless the Java parasites could check the pest.

*This outbreak began in the areas marked H and K in Map 2, and the* position at the commencement of operations with *P. parvulus* was, briefly, that in these 2 areas maximum defoliation had already been reached and that the pest had already spread half-way across area B from K and had occupied about a quarter of the large area M from K. In these last two areas (B and M), however, the pest had not yet become abundant and the trees still looked healthy, except when closely examined. Another outbreak was in progress on the island Adavaci (J), which is almost covered with coconuts. All other parts of the estate were almost entirely free from the pest.

The area K, which is almost entirely bounded by forest, was selected for special observation purposes, the forest round it serving to confine the parasites at first and to prevent any appreciable immigration of pest or parasite individuals from elsewhere. The first liberation of *P. parvulus* in area K was made on 14th June, when early 1st-instar larvae were abundant and no other stage, except eggs, was present. This colony consisted of 500 adults, all of which were put on a small tree in the centre of the area. On 29th June, when the dominant stage of the pest was 2nd instar, 200 more parasites were liberated ou the same tree. No other liberations were made at any time in K, and the total number liberated was therefore 700 (of which 600 were females), and no other colonies were put out anywhere near K. On 29th June, 3 of the parasites were seen apparently ovipositing in 2nd-instar mines 5 minutes after they were liberated. Subsequently, for several weeks, nothing more was seen of *P. parvulus*, in *spite of almost daily inspection of the trees and dissection of sample larvae* and pupae.

The number of trees in area K is 1,340, and it was estimated that the average number of living pest individuals per tree was 4,000 in this generation. The total pest population for area K was therefore approximately 5 million. The parasites therefore had a tremendous task ahead of them. It was estimated, however, that after they had passed through only 2 generations, their population should be about 3 million, this estimate being based upon their biotic potential and life cycle, which were known, and upon the assumption that no unforeseen factor would arise.

By the end of July, no trace of *P. parvulus* had been found, except that one of the 3 larvae which the parasites were seen to attack on 29th June proved to be parasitised. This was not surprising because the adult parasites were presumably spreading and are much too small to be detected in trees like coconuts unless they are crowded. Moreover, although by this time many adult parasites of the first generation should have emerged, the generation could not yet have matured completely, since the oviposition period is long. On 2nd August, however, the first trace of the continued presence of the species was found, in the form of 3 dead and blackened larvae, which had died in the 2nd instar, and contained pupae of *P. parvulus*. These were found in a leaf which was cut from a tall tree close to the tree in which the species was originally liberated. No other larvae in the leaf which was cut were visibly parasitised, and the percentage was therefore extremely small and negligible. *This meant either that the species was not flourishing, or else that it had* spread very extensively. All the other larvae from the cut leaf were




MAP 2.—Rough map of Nabavatu, Fiji, showing Principal Coconut Areas. (Coconut *areas dotted, forested areas white.*)

dissected, however, and no less than 3 of them (all 3rd instar), although still alive, were found to contain young larvae of the parasite. This made the situation more promising, as it meant that the earlier adult parasites of the first generation had already started a second generation. It was estimated that the maximum population of adults which could be expected to be present by this time was 48,000, and that if these had spread widely the average number per tree would be about 35, which, in view of the fact that a tree contains about 6,000 leaflets and 4,000 *P. reichei*, could not be sufficient to render discovery easy. Further, these 35 had emerged from 5 hosts only (the usual number which mature in 2nd-instar hosts being 7), so that the average number of larvae already killed per tree at this time could not have exceeded 5, or 0·12% (5 in 4,000).

During August, parasitised 3rd-instar larvae or pupae were found in all parts of the area, though not in every tree. It was evident that *P. parvulus* had begun spreading as soon as it was liberated, and had continued to do so uniformly, and that although it was not detected in every tree it was nevertheless present in every tree throughout the whole area, the failure to detect it in certain trees being due to the fact that only a few leaflets were taken as samples from each tree. By the middle of August, when pupae were the predominant stage of the pest and the emergence of beetles had just commenced (see fig. 11), the parasite had spread to the boundaries of the area in all directions and had crossed the arbitrary boundary between areas K and B and penetrated about 20 yards into B. Except when it was first liberated, it was at no time more concentrated in the tree in which it was liberated than elsewhere. In 2 months, the parasite had established itself in about 1,400 trees and had distributed itself with remarkable uniformity throughout the area. Uniform spreading was its first activity, and no appreciable multiplication in any one tree took place until this had been accomplished. The remarkable rapidity and uniformity of the spreading was attributable to the fact that oviposition, particularly when only large hosts are available, is not continuous but takes place at long intervals; during the intervals, the parasite has no urge to oviposit or to remain in trees where it has found mines, and it merely feeds and wanders. On 23rd August, 1,000 pupal mines were collected from 5 typical trees representing all parts of area K, and 29 of these (*i.e.* 2·9%) were found on dissection to be attacked by *P. parvulus*, although only 6 were already dead. At this time it was estimated that the parasite should have multiplied to an extent equal to 2 complete generations and that its adult population should be about 160,000 for the whole area or 120 per tree. These 120 would have emerged from about 10 hosts (3rd-instar larvae and pupae), so that the host individuals already dead amounted to about 0·25% (10 in 4,000). Since the observed parasitism, including hosts not yet killed, was 2·9%, it was clear that a third generation had already commenced.* It was also clear that the parasite was not suffering any appreciable check in its new environment.

The beetles began to oviposit early in September. The hatching of their eggs was awaited with special interest, since it would decide whether *P. parvulus* could survive the period when only adults and eggs were

* Complete overlapping of generations necessarily prevailed.

present. During this period, no adult parasites were seen, but, as before, this was not surprising. The first eggs hatched on 26th September, and by 4th October 1st-instar larvae were abundant. On 4th October, 6 adults of *P. parvulus* were seen ovipositing on one leaf of a tall tree in the centre of the area. This observation alone meant that *P. parvulus* would be completely successful, for it showed that the obstacles which hamper *Elasmus* had been overcome. Forty-seven young larvae were collected from this leaf and immediately dissected, and 14 of them were found parasitised, all except 3 containing eggs only. Since many eggs had not yet hatched, this did not guarantee a high percentage parasitism in the young larvae, but it was nevertheless eminently satisfactory. On 5th October, 112 of the newly-hatched larvae from another leaf of the same tree were dissected and 37 were found to be parasitised (*i.e.* 33%), but on 12th October, when almost all the pest eggs had hatched, the parasitism in the same tree was only 19% (107 in 564 dissected). This meant that the larvae had appeared at a rate such that the parasites could not maintain the initial percentage. The parasitism did not fall below 19%, however. This percentage is high as compared with that observed at the end of the previous pest generation, and the reason for this is that the number of eggs which the parasite lays in small larvae is very much smaller than in large larvae or pupae, so that any one individual can destroy far more small larvae than large ones or pupae. The pest population was not greater in the new generation, because of the usual spread of the beetles.

First-instar larvae were dissected every day at this time, and it was found that no eggs of *P. parvulus* were present after 12th October. This meant that all the adult parasites which had been waiting to oviposit during the periods of predominance of beetles and eggs had now laid all their eggs and died, and that the whole of the parasite population was now represented by larvae (and perhaps a few pupae) inside their hosts. No increase in the percentage parasitism was therefore to be expected for some time, and none occurred. The sudden cessation of oviposition by *P. parvulus* in the young larvae was exactly comparable to that of *Oligosita* in the eggs, and the reason was the same in both cases.

The period of 2nd-instar predominance of the pest began on 30th October, and the bulk emergence of *P. parvulus* from the 1st-instar larvae began at almost the same time. At the beginning of November eggs of *P. parvulus* again appeared in the larvae (1st and 2nd instar). Throughout November, however, parasitised larvae (other than 1st instar already dead) were very rare, and this was due to the fact that the adult parasites did not oviposit heavily over a short period of time, as in the 1st-instar larvae, because they had not been waiting at all before being able to commence. Instead, each one oviposited irregularly and at long intervals. Meanwhile the pest individuals were getting larger and the number killed by each adult parasite was getting correspondingly less since the number of eggs laid in each host was much greater. For these reasons, no rapid increase in the percentage parasitism could be expected until the host individuals reached the 3rd instar, when the number of eggs laid per host would not further increase extensively.

At the beginning of December, pupae predominated. By this time, the first generation of parasites in this generation of the pest had already

laid most of their eggs, and adults of the second generation were already emerging. From this time the percentage parasitism increased very rapidly, as more and more of the second generation of parasites emerged. The increase was extremely spectacular. On 10th December the parasitism reached 50%. On 19th December it reached 100%. That is to say, on 10th December healthy pupae were abundant, but 10 days later, not a single one remained unparasitised in any part of area K. It was estimated that *P. parvulus* destroyed 4 million individuals in this one pest generation, and that 3 million of these were destroyed between 1st and 19th December.

Before parasitism reached 100% in the pupae, however, a few adult beetles emerged. The beetles first appeared on 3rd December, and they continued to emerge in small numbers until 19th December. Counts showed that 12% of the pupae produced adults before the parasites prevented any further emergence. Thus, although 100% parasitism was attained in the pupae, the parasitism for the whole generation was not more than about 90%.

The few adult beetles that emerged oviposited in due course, but since the number of eggs laid was extremely small as compared with the normal number, *Oligosita* destroyed almost all of them. This was a most interesting development. In nearly all the trees, parasitism by *Oligosita* was 100%, so that no eggs hatched, but in a few trees here and there, one or two mines were subsequently found, and every one of these was attacked by *P. parvulus*. This occurred in January. It was certain, however, that even if all the eggs had hatched, *P. parvulus* would have wiped out the pest completely in this area almost at once. *P. parvulus* proved capable, in 2 pest generations, of increasing from 700 to at least 30 million * in area K alone. The total increase from the original 700 was very much more than this, because the parasites spread extensively to other areas.

The 30 million or more parasites, which emerged from their hosts towards the end of December, had nothing to attack in area K, and the majority spread to other areas. They swarmed through areas B, H, M, E, aud N, and even reached D, G, X, Y, and the island J. The pest, by this time, had itself spread enormously, having attained the stage of maximum population throughout B and almost throughout M, and having become common in the southern end of F and in E, D, and G. In January, a few pest individuals reached the extreme western end of C, and the extreme southern end of A. The parasites which followed the pest to most of these areas, though exceedingly numerous, were not common in any one tree on account of their very extensive distribution. They were, however, sufficiently common to attain 100% parasitism in one pest generation. In all these areas, the beetles oviposited in January. At the beginning of February, when 1st-instar larvae predominated, parasitism did not exceed 10% except in those parts of B and M near to K. But at the end of March, when late 3rd-instar larvae predominated and a few pupae were present, parasitism averaged no less than 94% for all the areas and was nowhere less than 70%. This increase was even more rapid

* Estimated from counts of the number of pupae per leaf and the number of parasites per pupae.

than that previously observed in K, and this was due to the fact that the parasite was no longer spreading extensively, having covered almost all the areas reached by the pest. 100% parasitism was reached everywhere by the first week in April, and in some localities sooner. and hardly any of the pest individuals escaped long enough to pupate, and not one became adult. The whole outbreak was completely and effectively stopped.

At the end of March, *P. parvulus* reached the western end of area C and completely destroyed all the larvae which resulted from the few beetles which reached there in January. These few beetles would ordinarily have been the beginning of a severe outbreak which would have swept throughout the whole length of C. The whole of A and the greater part of F were saved similarly. The spread of the parasite to C was a remarkable achievement, as C is separated from all other areas by wide stretches of forest and by a deep inlet. The complete elimination of the pest on the island J, where beetles were extremely abundant in January, was similarly remarkable. But the parasite's greatest achievement was that of reaching the small neck of land Z (in March), where there are 2 small beaches and a few coconut palms in which the pest was common. This locality is separated from all other parts of the estate, except J, by a very steep and densely-forested slope, and it is separated from J by sea. No barriers of any kind, or any extent, were sufficient to hinder the parasites, either at Nabavatu or elsewhere.

In all localities, the most striking features were the suddenness and the thoroughness of the suppression of the pest. Both were due to the number of parasites per host. As an example of the suddenness, we may consider the case of 100 pupae of the pest of which 10 are parasitised. Since the parasitism is only 10%, the parasite cannot be said to be exerting any extensive influence upon the pest. Each pupa, however, yields about 17 parasites, so that about 136 parasites emerge, and of these at least 100 are females. These females at once begin ovipositing, and each one is capable of laying about 80 eggs and destroying at least 4 pupae. Actually, they are not required to destroy more than one each, and the consequence is that the parasitism in the 100 pupae jumps from 10% to 100% in a few days. The thoroughness was due similarly to the number of parasites per large host. When parasitism reaches 90%, for example, and the parasites emerge, the number of parasites is approximately 17 times that of the number of host individuals from which they have arisen and is 153 times that of the few pest individuals (the 10%) which remain alive. From this enormous excess of parasites, nothing can escape. They reach the pest individuals in the tallest and most exposed trees and the shortest and most sheltered; they find every mine in isolated trees surrounded by forest, and trees on small islands. They do not, however, find them all at the same time in all localities, and this is an important point in connection with the survival of the species.

The suddenness with which 100% parasitism was attained was most noticeable in the large area M, where the pest was particularly abundant and severe defoliation prevailed. At the beginning of March, the predominant stage was late 2nd instar and the parasitism varied in different trees from 31% to 52%. Most of the parasitised larvae, however, were still alive and feeding, so that at a glance there was no great reduction in

the pest's activities. On 20th March, when 3rd-instar larvae predominated, parasitism was 98%, but many parasitised larvae were still feeding. On 28th March, parasitism was 100% and nearly all the pest individuals were dead, but the parasites had not yet begun to emerge in bulk. On or about 1st April bulk emergence of the parasites began, and it continued for about 10 days. Counts showed that, in these 10 days alone, about 51,000 parasites emerged from every tree, and more than 200 million emerged in the whole of area M. They were to be seen every morning streaming out of the leaves in countless thousands, and the rate was about 5,000 per tree per day. Although this performance had been planned, as far as these things can be planned, in the course of 2 years' research, it was scarcely believable when it was actually witnessed.

Colonies of *P. parvulus* were liberated in several parts of the estate other than area K, but not soon enough to supplement the activities of the parasites from K. One colony (the first colony to be liberated in Fiji) was put out in area H on 26th May, but in extremely unfavourable circumstances. The parasites which comprised it were 50 adults more than 6 weeks old, which had been shipped as adults in Java, and in area H, when they were liberated, the predominant stage was adults, pupae were very rare, and there were no larvae at all and very few eggs. Yet the species succeeded in becoming established at once, and this was one of the most striking instances of its extreme hardiness and adaptability. The parasites in H, however, did not begin spreading until after those in K, partly because of the great initial disadvantages to which they were subjected and partly because H is entirely surrounded by forest; and they certainly did not spread soon enough to supplement the parasites from K appreciably, if at all. No parasites were liberated in A, D, N, G, X, Y, Z, or C, or on the island J, these areas being purposely left in order to test the spreading capacity of the parasite.

In all other localities and islands the results were almost the same as at Nabavatu, regardless of the size of the coconut areas. On the nearly circular island Kanacea, the circumference of which is about 8 miles, *P. parvulus* spread throughout the island, from a single colony of 600 individuals, in 6 months, and completely suppressed the pest in 7½ months; and this in spite of the fact that the island is almost entirely covered with coconuts, and in spite of the presence of the pest almost everywhere and in the condition of maximum population over a large area. *P. parvulus* was liberated at Kanacea on 28th August. The island was next visited on 2nd February, when the pest was found to have increased enormously. The parasite was found to be rare, and negligible as a control at that time, but it was present throughout the most severely attacked area. In the middle of April parasitism was 100% everywhere. The most rapid suppression of the pest took place at Tota, on Vanua Balavu, where a large coastal flat is covered with tall coconut palms and there are no patches of forest or other natural barriers. At Tota, 1,000 *P. parvulus* were liberated on 26th December, when a severe outbreak was developing throughout the flat and had reached the maximum in the centre. At the end of March, after only 3 months, 100% parasitism was observed everywhere except at one end, and here a few beetles had emerged. The progeny of these beetles, however, were certainly killed by

*Oligosita* and *P. parvulus*, although this was not actually observed because the locality was not visited again. This rapid suppression of the pest meant that in the period of one pest generation the parasite population had increased from 1,000 to at least 200 million. The result would not otherwise have been possible.

It was everywhere evident that if the parasites are already present in every tree (even if there is only one per tree) at the beginning of a generation of the pest, they can entirely suppress it before the end of that generation, and that if they are not uniformly present at the beginning they usually cannot attain 100% parasitism in one generation but can do so in two. On coastal flats, however, provided there are no natural barriers, 100% parasitism can be attained in one generation even though the parasites are not uniformly distributed at the beginning.

**2. Spreading to other Localities and Islands.**

The island Vanua Balavu is long and narrow, and of a peculiar shape. It is bent nearly at right angles in the centre, the two arms being directed roughly north-west and south-west. Its length from end to end, direct, is about 10 miles, but allowing for the bend, the length is about 13 miles. Excepting the greater part of the north-west arm, the island is almost completely fringed with coconuts, which, at many points, extend far inland.

*P. parvulus* was liberated in 8 different localities on the larger, coconut-fringed, part of the island, and the liberations were made in September (2), December (1), and January (5). By April the parasites had multiplied so greatly that they reached every locality throughout the island. They spread from place to place across belts of forest and areas of healthy palms, and it is almost certain that not one palm in which *Promecotheca* was present remained free from them. In this phenomenal spread they were undoubtedly assisted by the natives, who unintentionally carried them, as pupae, from place to place in the leaves used for making coconut-leaf baskets, and in other ways. Nevertheless, in view of the incredible numbers which emerged, there is little doubt that without any assistance they would have covered the island almost equally quickly. There were many other outbreaks as severe as the one at Nabavatu, and in every one of these the parasites emerged in March and April at the rate of thousands per tree per day.

The most remarkable instance of the exceptional capacity of *P. parvulus* for spreading was provided by the island Kaibu, which is very close to Yacata, and is 18 miles across open sea from Kanacea and 28 across the sea, via Kanacea, from the nearest point of Vanua Balavu. On 31st January, 1934, Kaibu was visited, in response to a rumour of a *Promecotheca* outbreak there. 500 adults of *P. parvulus* were taken ashore for liberation, none having been liberated there previously. A severe, but local, one-stage outbreak was found to be in progress. When leaves were cut from some of the trees, however, *P. parvulus* was found to be abundant already. The predominant stage of the pest at the time was late 2nd instar, and the percentage of larvae parasitised by *P. parvulus* was 52. It was certain that 100% parasitism would be attained before the end of the pest generation which was then developing, and that the

pest would be completely suppressed on this isolated island, without intentional human agency, only 10 months after the arrival of the parasite in Fiji from Java.

Kaibu and Yacata are very seldom visited, even by natives. It was found on inquiry, however, that a small sailing-boat went from Lomaloma (on Vanua Balavu) to Kaibu during October, 1933, or about that time (dates are immaterial on Kaibu), and there is therefore little doubt that *P. parvulus* travelled in that boat, either as adults which flew on board while the vessel was at anchor near the beach at Lomaloma, or, more probably, as pupae in mines in coconut-leaf baskets which were made from leaves cut at Lomaloma. The percentage parasitism observed at the end of January, in conjunction with the stage of the pest, confirmed the view that the parasite first reached the island in or about October. It could not, in any case, have arrived earlier, since it was not common at Lomaloma, or anywhere else in Fiji, until October, and was not liberated anywhere (except at Nabavatu) until the end of September. It is absolutely certain that the parasite was never taken to Kaibu or Yacata intentionally. There is a very remote possibility that it was carried by the prevailing easterly wind from Vanua Balavu or Kanacea, but in view of the distance this theory is exceedingly improbable. However this may be, the case of Kaibu demonstrated in a spectacular manner the extraordinary hardiness of the parasite and the ease and rapidity with which it can spread in existing conditions; and it also demonstrated the impossibility, again in existing conditions, of controlling the transference from island to island of insects of any kind, beneficial or noxious. It was already known that many outbreaks of *P. reichei* were due to the unintentional introduction of the pest by the natives, but it now seems probable that in future they will unconsciously transport the cure also.

### D. The Permanence of the Control exercised by *P. parvulus*.

*P. parvulus* was completely successful in suppressing the outbreaks which were progressing at the time of its introduction. The success of a parasite used for the control of a pest depends, however, upon its ability, not only to suppress severe existing outbreaks, but also to maintain the pest population permanently below the level of economic importance, either by maintaining it at a constant low level or by suppressing all future incipient outbreaks almost as soon as they arise. It does not follow that a parasite that can flourish in a new environment when its host is abundant will survive when its host is rare or absent, or will be able, even if it does survive, to multiply greatly until its host has itself become so numerous as to cause extensive damage. *P. parvulus* has yet to demonstrate its ability to prevent outbreaks in the future.

There are comparatively few parasites that can completely exterminate a pest over a wide area, but *P. parvulus* can do so. A parasite which lays only one egg on or in each host individual, and therefore can never exceed in numbers the host individuals which it kills, is less likely to become sufficiently numerous to find and destroy all the host individuals at one time than a species which, like *P. parvulus*, lays many eggs in

each individual. It was evident at Nabavatu that *P. parvulus* can become so excessively numerous that, in any continuous and uniform coconut area, not one larva or pupa of *P. reichei*, no matter how it is situated in the tree, can escape discovery by at least one parasite individual. In such an area, therefore, it is possible for *P. reichei* to be suddenly and completely exterminated, and the complete extermination of *P. reichei* can only result in the complete extermination of the parasite also. Moreover, the likelihood of extermination is greatly increased when the one-stage condition prevails, for if 100% parasitism is attained when large larvae and pupae only are present no more host individuals can appear subsequently, after the parasite population has been reduced by death and spreading. The extinction of the pest would be useless because it would be followed, sooner or later, by the accidental introduction of a few individuals from another island, and there would be nothing to prevent an extremely severe outbreak.

These questions were investigated at Nabavatu and elsewhere. It was realised that the parasite was liberated in conditions which were ideal for it, as regards the abundance and concentration of its host, and that it would subsequently be subjected to conditions so different that it might be unable to survive. That it would exterminate itself in certain areas by exterminating its host was evident. This, however, would be immaterial so long as the species did not disappear from other neighbouring areas at the same time, for its capacity for extensive and rapid spreading would ensure the reoccupation of the original areas as soon as the pest itself entered them. The problem therefore was, could the pest be exterminated in all parts of any one island at the same time? On very large islands, this was obviously impossible, but on small islands, not extensively divided by natural barriers into distinct areas, it did not seem impossible, theoretically, when the extreme abundance of the parasite in certain conditions was taken into account. The conclusion reached was that on small, flat, isolated, islands (such as coral islets) which are uniformly covered with coconut palms nearly uniform in height, the extinction of the pest and the parasite was possible and would occur, but only if the liberation or arrival of the parasite took place at a time when the pest was already abundant and in one-stage condition. If the pest were rare at the time of arrival of the parasite, extinction could not take place, because the parasites, being relatively rare also when distributed over the island, could not find the host individuals easily enough to parasitise all of them at the same time; and an unstable, but permanent, equilibrium would be established, the percentage parasitism varying directly as the concentration of the host. In any case, small islands such that extinction is possible in certain conditions are very few in Fiji and are of no importance.

On all larger islands extinction proved impossible, for two reasons. Firstly, the parasite cannot attain 100% parasitism in all localities at the same time; and secondly, it does not attain 100% parasitism in small trees, or trees sheltered by forest, quite so soon as in tall ones in the same area, and although in some areas the trees are all nearly uniform, in the majority there are many tall trees and a few small ones also. In the tall trees of the most recently infested area of a one-stage outbreak, 100% parasitism is reached one pest generation (*i.e.* 3½ months) later than in

areas in which the pest is already abundant, and in the small trees it is reached one generation later still. The reasons for this are that the parasites which attain 100% parasitism in the most recently infested area must be derived from those which spread from the other areas, and that the parasites do not descend in numbers to the small trees until they have destroyed almost all the pest individuals in the tall ones. This latter fact was noticeable in every area at Nabavatu. In the tall trees, the parasites multiplied sufficiently rapidly to destroy all the pest individuals before any of them could yield adult beetles; but in the small trees, although parasitism was high, a few beetles invariably emerged before the parasites had had time to attack all the mines. The beetles which escape in such cases are only a very small percentage (much less than 1%) of the total individuals present in the area. They are, in fact, comparable in numbers to those which are ordinarily present in non-outbreak conditions. Many of them spread because defoliation is heavy in the area in which they emerge. Some of them invade areas not previously attacked, where there are no parasites, and others remain where they are or spread to areas already severely defoliated but now devoid of the pest in consequence of the activities of the parasite. All of them lay eggs, but the resulting larvae survive only in the area which was previously free from the pest, and even here most or all of those in the tall trees are found by parasites that have survived from the previous pest generation in other areas. As before, however, some of the individuals in the small trees survive, and by this time the enormous excess of parasites which occurred several months previously in other areas has died out, without progeny in most cases. Both host and parasite are now rare and are present in comparable numbers, and as soon as this is the case a normal equilibrium is established. The writer left Fiji when this stage had just been reached in certain localities, and no further information is available. It is nevertheless easy to predict almost with certainty what the permanent position will be.

The pest and parasite will continue to exist everywhere, except possibly on certain small islets; and even on these islets the permanent existence of both could be ensured by the introduction of a few individuals of each at the same time, since extinction is only possible when the pest is already abundant when the parasite is introduced. The normal equilibrium between the pest and all its parasites will be similar to that which we have already described as being normally maintained by *Elasmus* and *Oligosita* only. In most localities, the indigenous parasites as well as *P. parvulus* will be present, and when this is the case, *E. hispidarum* will probably predominate, just as *D. javanica* predominates in Java, and exert the same degree of control as before. This means that on a few of the occasions when the pest reaches its maximum abundance, within the normal equilibrium, it will be sufficiently common to constitute multiple-stage outbreaks of negligible dimensions. In a few localities, however, *E. hispidarum* will be absent initially, as in the past, and this will occur principally when *P. reichei* is accidentally introduced into new localities. In such cases, *P. parvulus* will be present, or will discover the incipient outbreaks earlier than *Elasmus*, since its capacity for spreading and for finding host individuals when the host species is rare is much greater than that of the indigenous parasite; and consequently outbreaks

resulting from the accidental introduction of the pest will be more restricted and less frequent than before. One-stage outbreaks, which were the only ones for which control was urgently required, will never again attain serious dimensions. They can only arise from multiple-stage outbreaks. The mite will continue to cause the one-stage condition occasionally, but less frequently than before because multiple-stage outbreaks will themselves be less frequent. Immediately the one-stage condition is caused, *P. parvulus* will take over the control from *Elasmus* and the pest will be suppressed before it spreads at all. The activities of *Pediculoides ventricosus* will no longer be harmful. The phenomenal abundance of *P. parvulus* witnessed at the end of 1933 and early in 1934 will never again be possible, since *P. parvulus* will itself prevent its host species from becoming sufficiently wide-spread and populous. The lack of extensive one-stage outbreaks will render the accidental transference of the pest from one locality to another a comparatively rare occurrence, because it will rarely happen that leaves cut by the natives will contain mines.

Thus, there is every reason to believe that *P. reichei* is no longer a pest, and that *P. parvulus*, *E. hispidarum*, and *O. utilis*, will together control it permanently. It is noteworthy that *P. parvulus*, by itself, appears able effectively and permanently to control *P. reichei* in all existing circumstances, whereas the other two species, together or separately, are incapable of doing so in the presence of *P. ventricosus*. Moreover, although *O. utilis*, with *P. parvulus*, makes an excellent sequence of attack covering the whole of the development of *P. reichei*, no such complete sequence is necessary. The habit possessed by *P. parvulus* of attacking all the larval stages and also the pupa is the main factor in its success, and had it attacked only the larva or the pupa it would have been useless; but the additional attack upon yet another stage by *O. utilis* is superfluous from the economic point of view.

### E. *Promecotheca bicolor*, Maulik, as an Alternative Host for *P. parvulus*.

*P. parvulus* has an alternative host in Fiji in the form of *P. bicolor* (Plate XX). This Hispid is known only from Fiji, and very probably occurs nowhere else. It was first discovered in 1928, near Suva (Viti Levu), by R. W. Paine, who has since found it on Vanua Levu also. It feeds, as a larva and as an adult, upon at least two species of *Flagellaria*, but it does not occur wherever its food-plants grow. It is, in fact, a very local species, and it certainly is not present on all the islands of the group. It appears not to be present in Northern Lau, where a thorough search was made for it in 1933 by the writer without result, although one of its food-plants is common on several of the islands. The habitat of *P. bicolor* is totally different from that of *P. reichei*, since the species of *Flagellaria* are largely confined to the forest, where they climb, often to the tops of the trees, amongst a great variety of vegetation, but are seldom present in profusion. *P. bicolor* is seldom abundant, even in the localities in which it habitually occurs, being effectively controlled by the two indigenous parasites, *O. utilis* and *E. hispidarum*, which attack *P. reichei*. The equilibrium

between *P. bicolor* and these 2 parasites is comparable to that which normally prevails, in the absence of *Pediculoides ventricosus*, between *P. reichei* and the same parasites: that is to say, the equilibrium is unstable, the host multiplying periodically and at long intervals, and only occasionally becoming sufficiently abundant to damage its food-plant appreciably, and then only very locally. The one-stage condition appears never to occur in *P. bicolor*, and the equilibrium is therefore constant, except for variation within the normal limits of its instability, the parasites being able to breed continuously. This constancy contrasts strikingly with the complete unbalancing of the equilibrium between *P. reichei* and the parasites which results from the interference of *P. ventricosus*. The fact that *P. bicolor* is unable ever to become much more numerous than its parasites implies that *P. ventricosus* can never multiply sufficiently, as a parasite of *P. bicolor*, to affect the population of that insect appreciably because the forest habitat and mode of growth of *Flagellaria* spp. prevent the population of any insect on which *P. ventricosus* can feed from becoming dense enough for the mite's requirements. In these circumstances the parasites, as enemies of *P. bicolor*, can never be hindered by the mite, directly, or indirectly through the one-stage condition, as they are as enemies of *P. reichei*.

*P. bicolor*, like all species of *Promecotheca*, is a true leaf-miner, and its habits are very similar to those of *P. reichei*. The most notable difference, apart from food-plants, is that the egg-capsule of *P. bicolor*, which is larger than, but otherwise similar to, that of *P. reichei*, covers 2 eggs. The 2 eggs are placed one above the other, one being sunk into the leaf tissues and the other being wholly outside the leaf. The eggs are separated by a thin layer of excrement. The resulting larvae make a very large mine, and pupate within it. The adults, whose colouring is very similar to that of *P. reichei* but even more brilliant, are not gregarious. They feed in precisely the same manner as *P. reichei*.

It is not yet absolutely certain that *P. parvulus* will attack *P. bicolor* in the field, as no parasites were liberated in localities where this Hispid occurs until a few days before the writer left Fiji. In the laboratory, however, *P. parvulus* attacked larvae, prepupae, and pupae very readily and developed normally therein, and there can be little doubt that *P. bicolor* will prove to be an alternative host in the field. In the forests in Java, *P. parvulus* appears to seek its hosts only in Zingiberaceous plants, in which various Hispid species abound, but in Fiji there are no Hispids in Zingiberaceae; and *P. parvulus*, which has shown itself to be very readily adaptable to new environmental conditions, is likely to adopt *P. bicolor* as a normal host, in the absence of Hispids in the plants which it has hitherto been wont to frequent.

The importance of the alternative hosts in Java has already been mentioned. *G. xanthomelana*, by attacking bananas and other plants, enables *P. parvulus* to be much more generally distributed throughout the country than it would be if, like *D. javanica*, it attacked *P. nuciferae* only. The presence of alternative hosts serves to ensure the presence of the parasite in almost any locality in which *P. nuciferae* may appear, particularly as one of the food-plants of *G. xanthomelana* is the ubiquitous banana, which is very commonly grown beneath, or in the neighbourhood

of, coconut palms. In Fiji, *P. bicolor* will serve a similar purpose, but not to the same extent. The habitats of the coconut palm and *Flagellaria* spp. are absolutely distinct, and on large islands a colony of *P. bicolor* may be separated by several miles from the nearest locality where *P. reichei* could establish itself. *P. bicolor*, therefore, as a source of parasites to attack *P. reichei*, will not be so readily available as is *G. xanthomelana* as a source of parasites to attack *P. nuciferae*. Nevertheless, there are many coconut estates in Fiji which are bordered or divided by belts of forest in which *Flagellaria* grows, and *P. bicolor* can definitely be expected, in many coconut areas, to enable *P. parvulus* to be present and available in more localities than if *P. reichei* were the only host.

In the Lau Group, *P. bicolor* is apparently absent, and *P. parvulus* has no alternative hosts. On this account, the introduction of *P. bicolor* was considered as a means of increasing the efficiency of the parasite as a control for *P. reichei*. The conclusions reached at the end of the work in Lau, however, indicated that *P. parvulus*, as we have already recorded, will survive, with only *P. reichei* as host, in a sufficiently large number of localities on each island to ensure its reaching any area into which *P. reichei* may be accidentally introduced. In these circumstances, *P. bicolor* will be unnecessary, but it is important to note that should it prove desirable, at any future time, to increase the economic effect of *P. parvulus* in Lau, this can be very easily and quickly done by the simple expedient of introducing *P. bicolor* from Viti Levu, where it is always available in the forest near Suva. In Lau, *Flagellaria* is in closer association with coconut areas than in many other parts of Fiji, since the estates consist, for the most part, of numerous comparatively small areas separated by virgin forest. The utility of *P. bicolor* would, on this account, be greater in Lau than elsewhere.

In the course of the investigations in Java, the possibility of introducing an alternative host from that country was considered. The only available hosts were *P. nuciferae*, *G. xanthomelana*, and certain Hispids that live only in the forests on Musaceae and Zingiberaceae. The forest Hispids obviously could not be expected to be more useful than *P. bicolor*, except that the introduction of a species feeding on Zingiberaceae would tend to make *P. parvulus* slightly more generally distributed in the forests than it can be with *P. bicolor* alone as host. The introduction of *G. xanthomelana*, on the other hand, would greatly increase the prevalence of the parasite, in coconut areas, as bananas are present in every native village and on all coconut estates. The introduction of this Hispid would be an absolutely safe procedure, in spite of the fact that bananas are economically a very important crop. It is absolutely certain that *G. xanthomelana*, while serving a useful purpose as an alternative host, would be maintained permanently in a condition of harmlessness and rarity by *P. parvulus*. It would, in fact, be even more effectively controlled than it is in Java, where the effect of *P. parvulus* is appreciably, though not seriously, diminished by secondary parasites. Public opinion, however, would render the introduction of an insect which attacks bananas virtually impossible, except as a secret procedure, no matter how thoroughly the consequences could be predicted by experts. With regard to *P. nuciferae*, it is interesting to observe that the introduction of this species into Fiji

(*i.e.* the introduction of a recognised coconut pest) would be entirely harmless, in the presence of *P. parvulus*, and would ensure the maximum efficiency of the parasite, provided only that the Fiji climate were not detrimental to the Hispid. Again, there would be an uproar from the general public, but the fact remains. The one-stage condition is impossible, except very temporarily, in *P. nuciferae*, and the presence of this species in Fiji would ensure that all the parasites could breed continuously and were more generally distributed at all times than they could be in any other circumstances. Although it is exceedingly improbable that it will ever be necessary to take further measures against *P. reichei*, it is desirable to notice at this point that the correct procedure, if such a contingency arose, would be to introduce alternative hosts, not to introduce other parasites.

The control of *Levuana iridescens* and of *Aspidiotus destructor*, which were formerly very serious coconut pests in Fiji, was effected by the introduction of natural enemies from Malaya and Trinidad respectively. The permanence of the control in both cases was attributable in a large measure to the presence in Fiji of alternative hosts for the introduced enemies. The alternative hosts, in each case, differed bionomically from the pest for which the introduction was made, in a manner such that they could not be so completely suppressed as the pest; and they therefore served to enable the introduced enemies to survive in localities where the pest was exterminated and to be generally distributed, regardless of the pest. In the case of *Levuana*, another useful purpose which the alternative hosts of the parasite served was to enable the latter to breed without interruption at times when a partial one-stage condition of *Levuana* would otherwise have prevented continuous breeding. The permanent control of *P. reichei*, however, does not depend to the same extent upon alternative hosts for the parasite employed. That *P. parvulus* is not appreciably handicapped by the one-stage condition is already obvious; and its long adult life, its habit of pairing as soon as it emerges from its host, its ability to utilise, for breeding purposes, all stages of its host except adults and eggs, and its ability to mature in numbers in a single host individual, make it capable of surviving in conditions of host scarcity which would be fatal to many other parasites. *E. hispidarum* and *O. utilis*, which almost certainly have no alternative hosts other than *P. bicolor*, usually appear, sooner or later, wherever *P. reichei* itself appears, and for surviving adverse conditions of this nature they are much less suitably adapted than *P. parvulus*. Thus, there is every reason to believe that *P. parvulus* will prove sufficiently effective in existing circumstances, and that although its effectiveness could be increased by the provision of other hosts, no such measure is needed.

### F. The Natural Enemies of *P. parvulus* in Fiji.

It was anticipated in Java, when the introduction of *P. parvulus* into Fiji was contemplated, that this parasite would be immune from attack by the natural enemies of the indigenous parasites in Fiji on account of its internal habits. This, however, did not prove to be the case. It was found that *P. parvulus* was attacked to a much smaller extent than *E. hispidarum*, but it proved by no means immune. As

soon as it became common in Fiji, about 3 months after it was first liberated, it was commonly attacked by the two Eupelmids, by *Tetrastichus taylori*, and by *Pediculoides ventricosus*.

The habits of the Eupelmids and *T. taylori*, as enemies of *P. parvulus* as well as *E. hispidarum*, have already been outlined. Although the Eupelmids and *Tetrastichus* were commonly found in this new rôle, the percentage of *P. parvulus* destroyed by them was absolutely negligible. The principal reason for their failure to avail themselves more extensively of the abundant supply of food provided by the introduction of *P. parvulus* was that they cannot easily find the parasitised *Promecotheca* individuals until these are really plentiful, by which time *P. parvulus*, on account of the large number of its progeny which can mature iu a single host, is about to become sufficiently numerous to suppress the pest. The secondary parasites begin to multiply too late to derive any benefit from the advantage provided by the abundance of food. As soon as they begin, the abundance gives place to scarcity or absence. Contributing factors in the case of *T. taylori* are that, as a general rule, only a small percentage of the *P. parvulus* individuals present in a large larva or pupa of *P. reichei* is attacked at any one time, so that the majority produce adults in due course, and that *P. parvulus* is liable to be attacked for only a short period of its development (*i.e.* as a full-grown larva or prepupa). In these circumstances, the percentage of *P. parvulus* destroyed must always be low, and it must, in fact, be much lower than the percentage of *Elasmus* destroyed, since the latter is much more readily available, being external, and does not develop in such large numbers in each mine which it attacks. *Elasmus* can suppress multiple-stage outbreaks in the presence of the secondary parasites, and its impotence in one-stage outbreaks is not due to the secondaries. *P. parvulus*, therefore, will never be seriously hampered by them—much less seriously, indeed, than it is by its indigenous enemies in Java, and even these do not render it economically ineffective.

*P. ventricosus* attacked *P. parvulus* abundantly as soon as the latter became sufficiently plentiful. It was estimated, in August, 1933, at Nabavatu, that in many trees 80% of the *P. parvulus* were destroyed by *P. ventricosus*. At this time *P. ventricosus* was destroying a very high percentage of *P. reichei*, as is its wont towards the end of the dry season. It was evident that the actual percentage of *P. parvulus* attacked, however high, was immaterial so long as it did not exceed the percentage of *P. reichei* attacked; and that if the percentage of *P. parvulus* destroyed, even though it were 80, were less than the percentage of *P. reichei* destroyed, the activities of the mite would actually be beneficial. This was, in fact, the observed result of the mite's activities. The mite entered the mines at random, regardless of their contents, and it attacked every living organism that it found inside them. It destroyed healthy larvae and pupae of *P. reichei* and it destroyed, and to an equal extent at any one time, *P. reichei* individuals which were parasitised by *P. parvulus* but were still living, killing the contained *P. parvulus* larvae indirectly. But its entry into the hard skins of *P. reichei* containing *P. parvulus* prepupae and pupae was only possible by way of the minute punctures or fractures which apparently serve for the entry of air, and in many cases these were too small and in all cases they were not easily found.

Moreover, the mite, on entering the skin, was faced with a large number of *P. parvulus* individuals, and it could only attack one. It attacked one, and this one died. The mite matured in due course and gave rise to many others, but by this time the other *P. parvulus* had very often emerged. In very many instances, on the other hand, the mite produced its offspring before the other *P. parvulus* individuals matured, and the young mites spread throughout the *P. reichei* skin and killed every one of the *P. parvulus*, the host skin becoming absolutely full of *P. ventricosus* spheres of all sizes. It was found, however, that the parasitised *P. reichei* individuals in which all the *P. parvulus* were destroyed did not outnumber those in which only one or a few were destroyed. The ultimate result of the activities of *P. ventricosus* was that both the pest and the parasite were enormously reduced in numbers, but in the resulting populations the number of parasites, expressed as a proportion of the number of *P. reichei*, was slightly higher than it would have been if *P. ventricosus* had not appeared.

### G. The Results of the Introduction of *P. painei* and *D. javanica*.

The results of the introduction of these two Java parasites were nil, as was to be expected.

In the case of *P. painei*, only 3 males and 11 females were landed at Nabavatu, the species having failed to breed en route. These were liberated as soon as possible after arrival, actually on 27th May, 1933, on the island of Adavaci (J, Map 2). The predominant stage of the pest at this time on Adavaci was adults and eggs, and pupae were extremely scarce. The conditions for *P. painei* were therefore very adverse. Nevertheless, in spite of the scarcity of hosts and the age of the parasites, it is probable, judging from results obtained with *P. parvulus* in similar circumstances, that *P. painei* succeeded in finding hosts. It almost certainly did not establish itself for more than one generation, however, as there were no more pupae until August and these were very heavily attacked by *P. ventricosus*. It is probable, assuming that the parasites liberated succeeded in finding hosts, that a few *P. painei* survived until August and oviposited, but their numbers must then have been greatly reduced by the mite. Further, the almost complete elimination of the pest in the following generation by *P. parvulus* finally removed all opportunity for *P. painei* to become established. Whatever the reason may have been, no trace of it was ever found, and it is certain that it could never have been much use in Fiji because, like *E. hispidarum*, it would have been permanently hampered by the one-stage condition of its host, in conjunction with its habit of attacking one stage only.

*D. javanica* was reared in the laboratory at Nabavatu for many generations with *P. reichei* as host, and was liberated in considerable numbers. It was reared continuously from the time of its introduction in May, 1933, until April, 1934, when the work at Nabavatu was terminated. During this time, about 4,000 individuals were reared by the method described in Section IX, and of these, 3,635 were liberated. Of those liberated, 260 were put out at Kanacea on 25th August, 600 at

Munia on 16th September, and the remaining 2,775 at Nabavatu between 27th May and 1st September in 3 different places and 11 colonies.

The breeding work showed that *D. javanica* was not adversely affected by the climatic conditions in Fiji and that it could flourish with *P. reichei* as host. Nevertheless, no trace of it was ever found in the field in Fiji, in spite of the very careful inspection which was maintained throughout the year following its introduction. On many occasions when the parasites were liberated, the conditions, as regards the required stage and the numbers of the host, were ideal, and the failure to recover the species, even in the form of a single individual, was a little surprising. There is no reason to suppose in this case that the species failed to become established, and its disappearance was probably temporary only and attributable to very extensive dispersal and to the adverse effect of the one-stage condition of its host. *E. hispidarum* was rare in all the localities in which *D. javanica* was liberated, as in every locality where the one-stage condition prevailed. *D. javanica*, which has almost identical habits, therefore could not be expected to become any more common than *Elasmus*, and the factors which held *Elasmus* in check hampered *D. javanica* similarly from the first. Thus, although it was surprising that not one individual was recovered, there was no reason to expect *D. javanica* to attain even 1% parasitism in the time available to it prior to the complete suppression of the host species by *P. parvulus*. It is probable, however, that after two or more years, when the new equilibrium is established, *D. javanica* will be found to be present to the same extent as *E. hispidarum*, having become sufficiently widely distributed, before *P. parvulus* reached its climax, to survive the resulting extreme scarcity of its host. There is no doubt whatever that it will always be useless in one-stage outbreaks. The failure of *D. javanica*, the predominant parasite in Java, to reappear in the field in Fiji, while *P. parvulus* not only reappeared but completely suppressed *P. reichei* and attained a population of hundreds of millions in doing so, afforded striking proof of the differeuce in the effect of the new conditions on these two parasites and of the necessity for basing the selection of parasites for biological control work upon accurate predictions of their activities in the new conditions rather than upon their observed behaviour in the countries in which they are found.

## H. General Considerations concerning Biological Control.

It is convenient here to consider briefly the general principles that should govern the selection of parasites for biological control, with special reference to the campaign against *P. reichei*. These principles are separately enumerated and discussed below.*

i. The ability of a parasite to control a pest depends primarily upon the rate at which the parasite can multiply, relative to the pest, in the conditions in which the pest occurs. The first essential, therefore, is to ascertain accurately the sex-ratio, duration of life cycle, and egg-capacity

* The principles as here outlined apply primarily to tropical insects only, and are based on conclusions reached after 9 years of study of parasites in a variety of tropical countries.

of the parasite and the pest, and this often involves extensive field work as well as laboratory investigations in order that due allowance may be made for inaccurate data, particularly as regards duration of adult life, which may be obtained in laboratory conditions. Unless the biotic potentials of host and parasite are accurately known, it is wholly impossible to obtain successful results from parasite introductions except by good fortune, and much time and money are likely to be wasted. The necessity for thus placing the work on a mathematical basis at the outset would seem to be obvious; yet the time has not yet come when this necessity is generally appreciated.

ii. If all stages of the pest do not occur simultaneously (*i.e.* if successive broods do not overlap), most parasites that attack only one stage would be useless, whether introduced singly, or collectively to form a sequence of attack. Only a parasite which develops abnormally slowly or lives as an adult for a period longer than that covered by the development of the host could be completely successful. If, on the other hand, all stages of the pest occur simultaneously, as must normally be the case in the tropics where breeding is not controlled by seasonal climatic changes, many parasites that attack only one stage would be successful even if introduced singly; the introduction of several to form a sequence would inevitably accelerate the control and could do no harm, but in most cases the desired result would not be attained much sooner (probably only one pest generation sooner) than by the introduction of only one species.

iii. The ideal parasite, whether the pest occurs in the one-stage or the multiple-stage condition, is one which attacks all the larval stages and also the pupa. This is a special instance of sequence of attack, and, in general, a sequence is important only if it is effected by a single species. In one-stage conditions, moreover, the only parasite which could control the pest is one which itself constitutes a sequence, unless a species which attacks only one stage, but has a phenomenally long life, is known. If both of these types of parasite are available the former would be likely to be much more effective than the latter, other things being comparable.

iv. It is most important, in selecting a parasite, to guard against the possibility of the parasite preventing itself from multiplying continuously through causing the one-stage condition in a pest which has not previously been known to occur in that condition. *P. ventricosus* as a parasite of *P. reichei* is an example. Another is *Ptychomyia remota*, the parasite which effectively controlled *Levuana iridescens*. In this latter case, the parasite caused a partial one-stage condition, and this was detrimental to it and beneficial to the pest in places where alternative hosts were absent, although fortunately these places were very few and the parasite, by finding alternative hosts almost everywhere, was very successful. Many other instances could be given of parasites which are incompletely effective as controls for this reason. It is not usually possible, in selecting the parasite in the foreign country, to predict with certainty whether it will cause the one-stage condition or not, but it is possible to select a parasite which will be able to survive in large numbers if it does cause this condition.

v. The question of alternative hosts must be considered, not only because they tend to ensure uniform distribution of the parasite and its continued presence in localities in which the pest is rare or absent, but also because they are one means of preventing the pest from benefiting in the event of the parasite causing the one-stage state. The introduction of alternative hosts should be undertaken if their presence seems desirable, provided every possible consequence is thoroughly studied first.

vi. It is unwise to assume that the parasite which is the most effective of several in its own country is, for this reason, the most desirable for introduction into another country.

vii. The possible consequences of competition must be considered. The probability of competition having serious results is usually over-estimated; nevertheless, competition can, in a variety of special circumstances, favour the less useful of two parasites. *P. parvulus* and *D. javanica* in Java are an example, although in this case the consequences are not serious because the species which predominates, although unable to suppress the pest so thoroughly as the other by itself, can do so sufficiently to satisfy economic requirements.

viii. One of the most generally accepted principles of biological control is that secondary parasitism must be avoided. This is obviously true in many cases, but it seems desirable to point out that the significance of secondary parasites in this respect is often greatly exaggerated. It is necessary to study the secondary parasites present in the country where the pest is to be controlled, as well as the indigenous primaries and the pest itself. Many secondaries are wholly incapable of hindering extensively the primaries which they attack, mainly because the percentage of primary individuals which they succeed in finding increases directly as the concentration of the primaries and the percentage cannot approach 100 until the primaries are already sufficiently plentiful to suppress the pest. In other cases, inferior egg-capacity, or other factors of this nature, may ensure economic negligibility in the secondaries. For these reasons it is unwise to refrain from introducing a parasite which seems otherwise desirable, and to search for another, merely because the former is certain to be attacked by secondaries which are already present. The elimination of the secondaries from the consignment of primaries introduced is an obviously desirable and usually simple precaution, but in many cases the introduction of the former would not be harmful to an appreciable extent.

ix. The thorough study of the primary parasites already present in the country where the control is required is often invaluable as a means of ascertaining what type of parasite is needed to succeed where they fail.

x. In many circumstances the number of individuals of a parasite species which mature in each host individual is a most important factor in the efficacy of the species as a means of control. A large number of individuals per host may be highly beneficial, enabling the species to survive more easily when its host is rare and to escape the attack of secondaries to a large extent by remaining relatively sparsely distributed until it suddenly becomes common enough to suppress the pest. In other possible circumstances, the presence of a large number of individuals

in each host might conceivably be harmful. In any case, however, the fact that only one host individual is destroyed when many might be destroyed is not of itself disadvantageous. It might result in the postponement of the suppression of the pest for one generation, but this is negligible. Its chief consequence is that the final suppression is much more thorough than it would otherwise be, and is very sudden.

## IX. METHODS EMPLOYED FOR BREEDING AND STUDYING *PROMECOTHECA* AND ITS PARASITES, AND FOR COLLECTING DATA IN THE FIELD.

### A. Breeding and Studying *Promecotheca* Spp.

*P. nuciferae* can be bred very easily in large cages containing growing seedling coconut palms. It oviposits readily on the leaves of seedling palms, and its larvae flourish in the leaves of such palms. *P. reichei*, on the other hand, cannot readily be bred in cages. It does not normally oviposit on small palms, and although it can be induced to do so, the resulting larvae die in large numbers, presumably because the leaves are too thin. In breeding *P. reichei*, therefore, it is always necessary to utilise some means of inserting the larvae into mature leaflets which can be kept in water, and of transferring them to new leaflets as occasion requires. Further, in the course of life-history studies of both species of *Promecotheca*, and in the course of studies of those internal larval parasites whose presence does not immediately prevent further development of the host individuals, it is necessary to remove the Hispid larvae from their mines every day for examination, and this involves frequent insertion of them into fresh leaflets in order that they may continue feeding.

Many different methods for making artificial mines for the insertion of larvae were evolved and tested, but only one proved satisfactory aud practicable on a large scale. The successful method consisted in the insertion of a needle at the edge of the coconut leaflet, between the two epidermal layers, for a distance of about 2 cm., and the subsequent rolling of the needle, first in one direction and then in the other, the point being kept stationary inside the leaf tissues. This, if properly executed, results iu a triangular incision, the apex of the triangle being directed towards the mid-rib and the base lying along the edge of the leaflet. The two epidermal layers are entirely separated without being fractured. This operation sounds comparatively simple, but in reality weeks of constant practice are necessary before the operator becomes adept and quick in performing it. Almost constant use of this method was made in Java in the course of the investigations already described, and the native employed for the purpose eventually became able to make 30 of these incisions per hour.

The larvae are caused to enter the artificial mines by the application of a needle to their posterior extremities after their heads have been placed in the openings of the mines. A paper clip is then placed on each mine in such a way that the larvae cannot escape. Larvae of all sizes can be inserted in this way, and almost all larvae resume feeding within an hour after insertion and continue mining in a normal manner. The leaflets containing the larvae are kept in water and a short length of their submerged ends is cut off every third day. In this way, leaflets from young leaves can be kept in good condition for 3 weeks if necessary.

There is no need to insert each larva into a new leaflet every time it is removed from its mine for examination. If the mine is opened carefully, the larva can be put back into the same mine many times before the mine becomes so extensively damaged that it cannot be used again. The best method for opening a mine is to insert sharp forceps transversely into it beneath the upper epidermis, and tear the latter across and along the sides of the mine so that a portion of it can be lifted as though hinged. The larva can then be shaken out, and can be reinserted after examination, the flap being closed with a paper clip. This method of opening and closing the mines was used, not only for the study of larvae, but also for the study of pupae and adults in their mines. The adult beetles often fail to emerge from the pupae if the latter are permanently removed from the mines, and it is therefore necessary to adopt some procedure of this kind whenever the development of individuals is being studied.

When mines are plentiful in the field near the laboratory, the making of artificial mines is unnecessary. The larvae which are being reared are simply inserted into mines in freshly-cut leaflets, the normal occupants of the mines having been removed. This method is much quicker and easier than making incisions with a needle.

Control experiments showed that the rate of development is not affected in any way by the transference to artificial mines, provided that the leaflets concerned are kept in fresh condition by the frequent changing of the water and by the periodic cutting of their submerged ends.

In rearing *P. reichei* from eggs laid on seedling palms, it is necessary to transfer the larvae at an early age to mature leaflets. Nevertheless, it is desirable to permit the larvae to mine in the leaves of the seedling palms for 3 days, though not longer, before they are transferred; otherwise they often prove too weak to begin mining in artificial mines.

Folded paper was often useful, in lieu of mines, for enabling the adult beetles to emerge normally from the pupae.

## B. Breeding and Studying *P. parvulus*.

*P. parvulus* can be bred very easily in laboratory conditions, the only requirement being an abundant supply of *Promecotheca* larvae or pupae and of glass tubes (of which the most convenient size is $4'' \times 1''$). The parasite performs all its activities in a normal manner in glass tubes, and in evolving methods for bulk-breeding the only factors to which it was necessary to give attention were the number of parasites per tube and the time during which the mines to be attacked were left in the tubes. Since the parasite does not oviposit every day, the insertion of only one parasite with each mine results in only a small percentage parasitism and in a slow and irregular output of adult parasites later. On the other hand, the insertion of a large number of parasites in each tube results in heavy superparasitism. In either case, much time and labour is wasted. Experiments showed that the best results were obtained by the insertion of 4 female parasites and one mine into each tube, the mines being left in the tubes for 2 days. It was found that the ages of the females used should not be less than 4 days if maximum parasitism was to be obtained, and that each set of females could be used 3 times, though not more,

without reduction in the resulting percentage parasitism. Thus, fresh mines were inserted into the tubes on the 3rd and 5th days; and on the 7th day new parasites as well as new mines were inserted. The number of tubes operated at one time was 20, in 2 sets of 10 each, the 2 sets being operated on alternate days.

This method yielded 90% parasitism and about 150 parasites per day if large larvae or pupae were employed as hosts. A yield of 150 per day was regarded as sufficient, but the method could obviously be extended indefinitely. The whole of the routine, as outlined above, was executed, in Fiji as well as Java, by a native, who was responsible also for feeding the parasites which emerged and were stored for shipment to other islands, and for inserting the parasitised individuals, if these were larvae, into artificial mines in fresh leaves on removal from the tubes. The mines were prepared for insertion into the tubes by cutting the leaflets containing them to suitable lengths and putting a paper clip on each end of each strip thus obtained. The paper clips served to prevent curling of the strips, and one of them also served to close the cut end of the mine. A drop of honey was placed on each strip to serve as food for the parasites. Pupae were used as hosts whenever they were available, as the necessity for inserting the parasitised individuals into new leaflets for feeding purposes was thus obviated. The pupae were removed from the mines when the mines were removed from the tubes; and they were then stored in bulk in other tubes, which required no attention until the parasites emerged as adults. The adult parasites were stored in similar tubes, about 70 being placed in each, and were provided, every third day, with fresh food in the form of honey. It was found that one trained native sufficed to attend, without assistance, to the bulk-breeding and feeding operations if the former did not involve the operating of more than 10 tubes per day, and if the latter did not involve more than 7,000 parasites. Supervision was required in order to ensure that the normal sex-ratio was maintained and that pairing took place before the females were placed in the breeding tubes, but otherwise no supervision was necessary. The fact that the females are much more strongly phototropic than the males was utilised in the periodic checking of the sex-ratio and rendered this checking a comparatively simple matter in spite of the small dimensions and great activity of the parasites.

The degree of dilution of the honey used for food was found to be of great importance. Too much or too little water caused the parasites to die prematurely. The best results were obtained by adding only just enough water to cause the mixture to flow rapidly, and this entails very slight dilution. It is unnecessary, however, to use any more accurate means of obtaining the most suitable degree of dilution. In the writer's experience, honey gives better results in tropical conditions than lumps of sugar, sugar water, raisins, or any other form of food commonly used for nourishing parasites in captivity. For all Chalcids, and most other Hymenopterous parasites, very slight dilution gives the most satisfactory results. For Tachinid parasites much greater dilution is necessary.

The study of the early stages of *P. parvulus* presented some difficulties because the rate of development varies with the stage of the host, and because the examination of the parasite larvae and eggs involves the

dissection of the host and the consequent death soon afterwards of the parasites themselves. The development of the parasite was studied by utilising *Promecotheca* larvae or pupae, whose history was known, as hosts, so that all the individuals of each batch used could be in exactly the same condition. Each individual of each batch was then inserted into a tube containing a single female parasite known to be ready to oviposit, and all the individuals of each batch were inserted into tubes with the parasites at the same time and left therein for the same period of time (usually 6 hrs.). Subsequently, a few individuals of each batch were dissected every 12 hrs., or as the investigation required, for the examination of the contained parasites. By combining all the observations thus made, a complete and accurate record of the whole of the development of the parasite was obtained.

### C. Breeding and Studying the External Parasites.

The external parasites (*D. javanica* and *E. hispidarum*) oviposit readily in mines in glass tubes. The method employed for the bulk-breeding of *D. javanica* consisted in placing one female parasite and one 3rd-instar mine in each of 20 tubes and removing the mines after one day only. New mines were inserted every day and the same parasites were used for 10 successive days. This procedure resulted in 70% parasitism and a yield of 80 parasites per day, provided that certain precautions (described below) were taken to ensure normal humidity in the mines. If more than one parasite is placed in each tube, or if the mines are left in the tubes for more than one day, excessive oviposition takes place and the yield of parasites is greatly lessened as a result of the premature death and drying of the hosts caused by excessive stinging, and also as a result of the abnormally large number of parasite larvae competing for the strictly limited food supply. Only 3rd-instar mines give satisfactory results. If 1st and 2nd-instar mines are used the hosts shrivel and die prematurely in large numbers, and this occurs in the field as well as the laboratory and cannot be obviated.

In order to ensure a constant yield of parasites, it was found necessary to devise some simple method of controlling the humidity in the mines after they were removed from the tubes. If the humidity was less than 70%, many host individuals dried prematurely. After much experiment, it was found that sufficiently constant humidity could most easily be obtained by placing the mines (as soon as they were removed from the tubes) upon flat sheets of wire gauze suspended horizontally about 1 cm. above the surface of water in shallow metal trays, the latter being kept in a corner of the laboratory which was not subject to strong draughts of air. It was found that the humidity just above the surface of the water was nearly constant and never fell below 70%, regardless of the percentage in the room as a whole. This simple method was so successful that it was adopted as a regular part of the routine, each batch of mines being left on the racks in the trays for 6 days after removal from the tubes. After 6 days, the contained parasites were full grown and no further control of the humidity was necessary. The mines were therefore removed from the racks at this time and stored in hulk in glass jars until the adult

parasites emerged. It seems hardly necessary to add that no modern methods for controlling humidity were available on the remote island where the work was conducted.

For detailed study of the development of *D. javanica* and *E. hispidarum*, it was necessary to rear the parasites in small glass cells, so that they could be watched constantly. It was found that the frequent opening of the mines which was involved in an attempt to study the parasites *in situ* nearly always resulted in the displacing of the parasites so that they could not resume feeding when the mines were closed again. It was also found that unless the parasites were enclosed between two surfaces in close proximity (like the walls of a mine) they could not easily find the host when they emerged from the eggs and could not feed normally even when they did find it or were placed on it. For these reasons, small cells were made by sticking circular rings of cardboard on to glass microscope slides, and the cells were closed by means of other slides clipped over them. The parasites to be studied were placed as eggs in the cells, together with their hosts, and their development could then be watched with ease. This method proved most satisfactory, provided only that if the humidity in the laboratory fell below 70% a drop of water was inserted between the slides so that it soaked into the cardboard. For the purposes of shipment to Fiji from Java, this method was the principal one employed, as it was impossible to be sure that the parasites were developing normally in the conditions prevailing on board ship if they were left in the mines. The method is laborious, because it entails opening every mine carefully before the parasite eggs hatch and removing each egg separately, under the microscope, with the point of a needle. It was found possible, however, to transfer 300 eggs per hour to the cells, 20 being placed in each cell with one paralysed host individual.

## D. Collecting Data in the Field.

The collection of data concerning percentage parasitism, pest and parasite populations, and so forth, presents certain difficulties in one-stage outbreaks. Except at the end of each pest generation, observations made at any one time are of little significance, because the various controlling factors operate successively, not simultaneously as in multiple-stage outbreaks. The control is cumulative in each pest generation, as in the case of a pest whose time of occurrence is determined by seasonal climatic changes in temperate countries. In these circumstances it is necessary to collect data frequently and regularly and to adopt some standard method of tabulating the data collected on the various occasions so that the cumulative effect of the various factors is shown.

In the method adopted in Fiji, sample leaflets were cut approximately every 3 days throughout each pest generation and the fate of all the pest individuals in the sample leaflets was recorded, care being taken to record only those that belonged to the current generation. All eggs except those that had hatched were dissected, and all mines except those that obviously contained living larvae were opened with sharp forceps for examination. The number of individuals recorded on each occasion was never less than 200 and was often more than 500, and it

was found possible to deal with about 200 per hour. In this way the fate of many thousauds of individuals in each period of predominance was recorded. The periods of predominance of the various stages (eggs, 1st instar, and so on) were considered as separate units, and mean estimates of the percentage destruction by the various factors and the percentage remaining healthy were obtained for each period by summing the data collected on all the occasions in each period. As soon as all the controlling factors were known and the symptoms of each could be recognised with certainty, a standard table was prepared to cover all cases and all periods, and all data were then entered in this table as soon as they were obtained. Thus, it soon became possible to obtain at a glance, or by a brief calculation, almost any numerical particulars which might be required, such as the pest and parasite populations at any given date, the rate of increase of any one parasite species, the cumulative effect of all the controlling factors up to any given time, or the extent of predominance of any one stage. Further, since the area and the tree from which each sample was taken were always recorded, it was possible to ascertain from the table the state of affairs at different times in certain individual trees and in the various areas into which the total outbreak area was naturally divided by the spread of the pest.

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PLATE I.

*Promecotheca reichei*; all stages, × 1·8. Top row, males; 2nd row, females; 3rd row, pupae (6 dorsal, 4 ventral); 4th row, prepupae (5 dorsal, 5 ventral); 5th row, 3rd-instar larvae (5 dorsal, 5 ventral): 6th row, 2nd-instar larvae; 7th row, 1st-instar larvae; 8th row, egg capsules on portions of coconut leaflets.

*All photographed immediately after having been chloroformed*: appearance typical of living specimens.

Plate 1.

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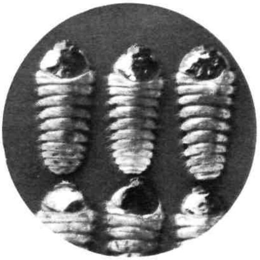
Plate II.

a.



b.

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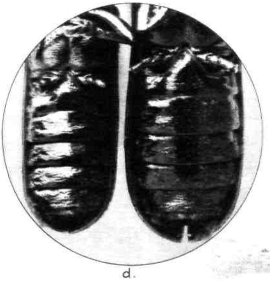
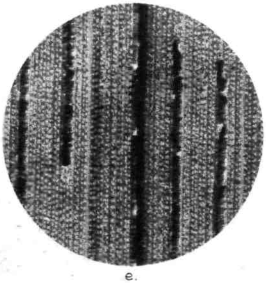


d.



e.

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## Plate II.

a, b, c, d, e, *P. reichei*; a, newly-hatched larvae, appearance typical except for slight dorso-ventral shrinkage; b, full-grown 1st-instar larva, just prior to cessation of feeding for moult, upper row dorsal, lower row ventral, appearance typical; c, 2nd-instar larvae, 1 day after resumption of feeding following moult, 2 dorsal and 1 (right) ventral, appearance typical except for slight contraction of prothorax; d, ventral view of abdomen of male (left) and female (right), hind legs removed, to show sexual dimorphism; e, feeding marks (fresh) of adult beetles on underside of coconut leaflet, the leaflet having been cut transversely across the feeding marks and the two portions placed side-by-side so as to show both the pointed and the square ends of the feeding marks.

All × about 9.

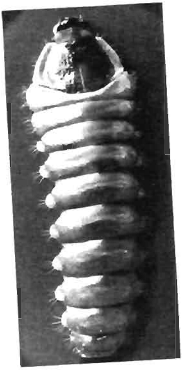
f. *Pleurotropis parvulus*; 4th-instar larvae removed from hosts, those in top row from larval host which had only just been killed by the parasites, others from larval host which had just been completely emptied by the parasites; × about 9.

PLATE III.

*P. reichei* ; a, full-grown 3rd-instar larva, dorsal ; b, ditto, ventral ; c, prepupa, ventral ; d, pupa, dorsal ; e, pupa, ventral. × about 9.

All photographed immediately after having been chloroformed ; appearance typical of living specimens.

Plate III.



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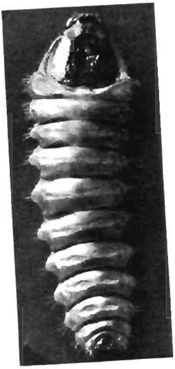

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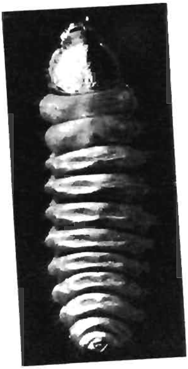

c

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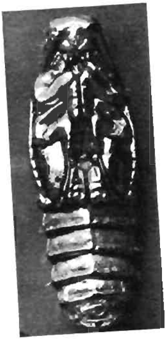

e

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Plate IV.

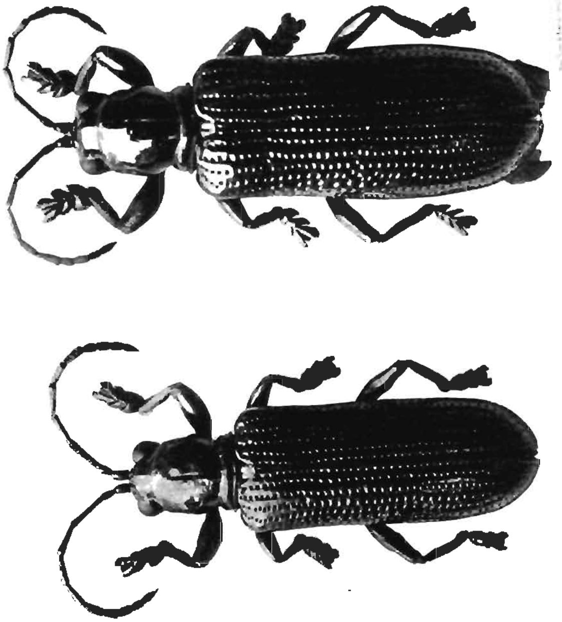


PLATE IV.

*P. reichei.* Typical male (left), and female (right); × 12. Different colouring of thorax and abdomen not indicated.

## Plate V.

a, *Oligosita utilis*; 3 parasitised egg capsules of *P. reichei*, reversed, with chorion dissected away ventrally, to show (upper capsule) 3 prepupae of *O. utilis* and (lower capsules) pupae of *O. utilis* (7 and 3), all in normal positions.

b, egg capsules of *P. reichei* showing (upper row) emergence holes of *O. utilis* and (lower row) holes made by predatory ants (which have completely removed anterior ends of the 2 capsules on right).

c, d, e, *Elasmus hispidarum* adults: c, male; d, female; e, large female and small male as seen by transmitted light (from a microscope slide).

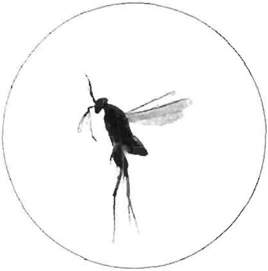
f, *Tetrastichus taylori*, adults, 2 females and 2 males (left and right).

All × about 9.

Plate V.

a

b



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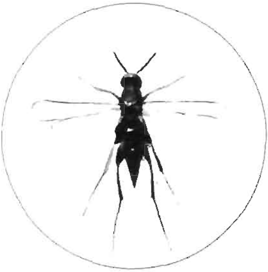

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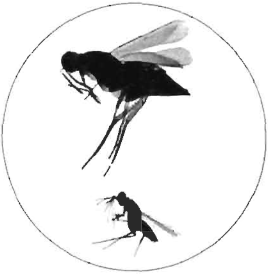

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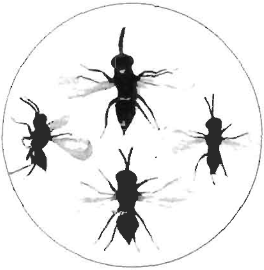
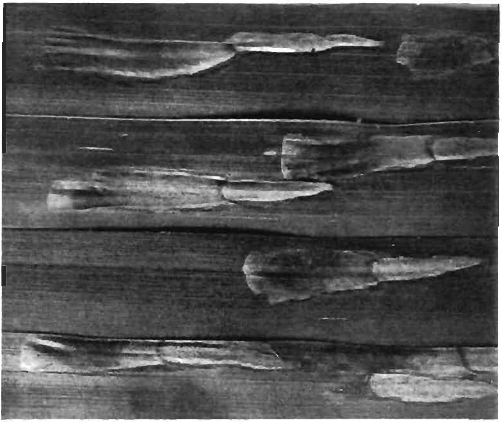
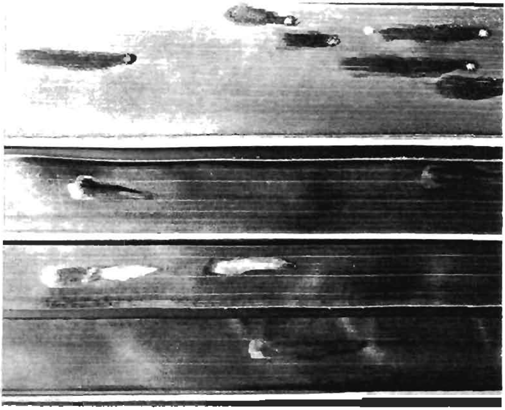


f.

Plate VI.



b.



a.

## Plate VI.

*P. reichei*, mines. a, portions of 3 leaflets, 2 upperside, 1 (right) underside, showing 1st-instar mines and egg capsules (one egg not yet hatched); largest mines full-sized for the instar.

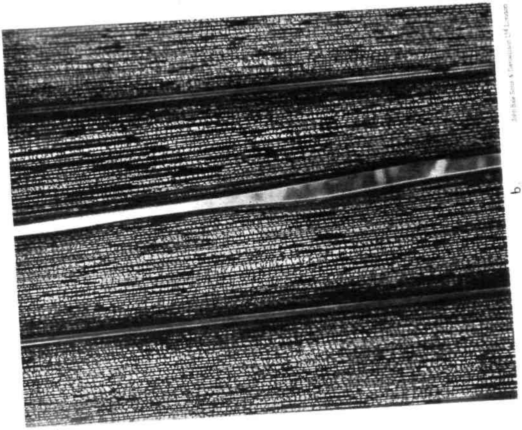
b, portions of 4 leaflets, all upperside, with 2nd-instar mines; the natural dark line terminating 1st-instar portion of each mine is clearly apparent, serving to show size attained by 1st-instar mine; larva in mine on right has ceased feeding for 2nd moult and a dark line of callous tissue is already forming across end of mine; larvae in other mines still feeding but nearly full-fed for 2nd instar (except one at left bottom corner).

## Plate VII.

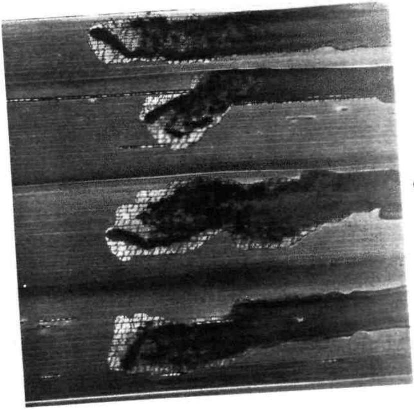
*P. reichei*; a. 4 3rd-instar mines (and a few old feeding scars of adult beetles) as seen when leaflets are held up against the light; the larvae were feeding normally when photographed, and are seen in silhouette at ends of mines, through the epidermis; excrement visible in silhouette behind larvae; veins and cross-veins in walls of mines visible as network: natural size.

b, portions of 2 leaflets covered with feeding-scars of adult beetles, as seen on underside when leaflets held up against light; upper epidermis still intact, with light shining through it; each incision is divided into sections by main cross-veins, which are not eaten.

Plate VII.



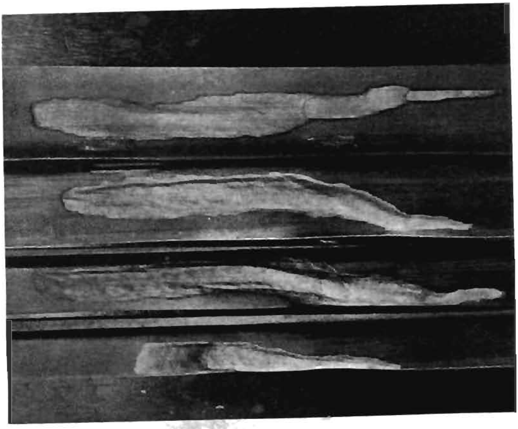
b



a.

Plate VIII

b.



a

Plate VIII.

*P. reichei*, mines. a, portions of 4 leaflets with 3rd-instar and pupal mines, 3 upperside, one (right) underside with capsule still present; mine on left early 3rd instar with larvae still feeding; others containing prepupae or pupae, walls of mines consisting throughout of dead tissue: transverse lines terminating 1st- and 2nd-instar sections visible, and similar lines round edges also visible, except at growing end of incomplete mine.

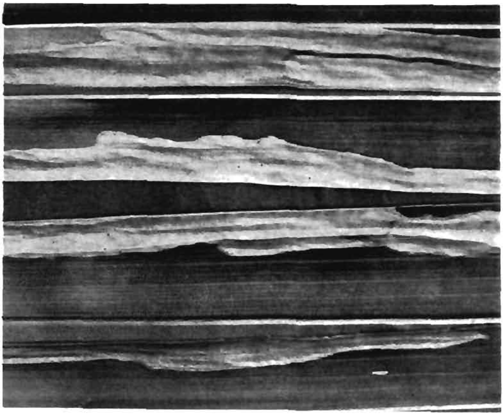
b, part of severely-mined leaf; mines nearly all pupal; note basal portions of leaflets devoid of mines.

PLATE IX.

*P. reichei.* a, mature mines, upperside, showing emergence holes of adult beetles; natural size.

b, pupal mines, upperside, parasitised by *P. parvulus*, showing (as small black dots) emergence holes of the adult parasites.

Plate IX



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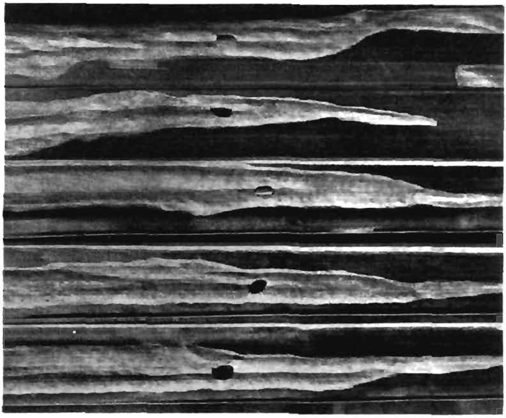
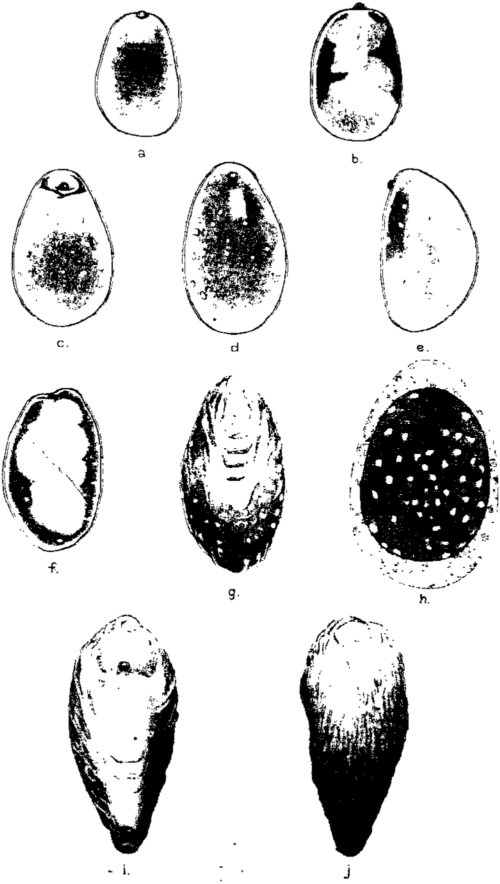


a

Plate X.

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## Plate X.

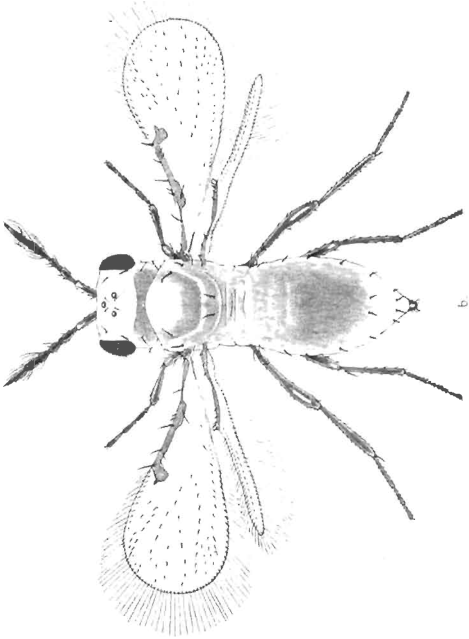
*Oligosita utilis.* a, larva 12 hours old (*i.e.* after hatching); × about 53. b, larva 2 days old: × 45. c, d, e, larva 4 days old: ventral view, contracted: ventral view, extended; and left lateral view, extended; × 45. f, larva $5\frac{1}{2}$ days old, ventral view, contracted; × about 38. g, larva 10 days old, ventral view; × about 38. h, same larva as g, same time, seen by transmitted light when compressed in water under glass cover-slip, dorso-ventral view: × about 38. i, j, larva 17 days old, ventral (i) and dorsal (j); × 45.

(All, except h, as seen by reflected light without compression; see also Plates V and XI and Text-fig. 8.)

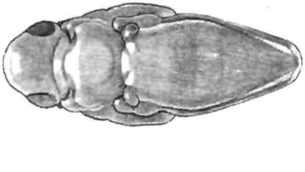
PLATE XI.

*O. utilis.* a, pupa, dorsal; × about 58.
b, adult female; × about 64.

Plate XI

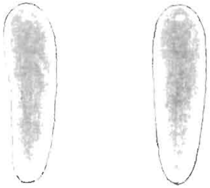


b



a

Plate XII.



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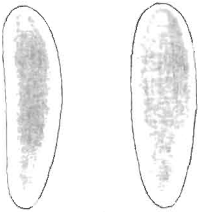


d

b

c

e.

f

PLATE XII.

a, b, c, *D. javanica*; a, egg, lateral and dorso-ventral, × about 110; b, newly-hatched larva, dorsal and left lateral, × about 160; c, full-grown 1st-instar larva. d, e, f, *E. hispidarum*; d, egg, lateral and dorso-ventral, × about 102; e, half-grown 3rd-instar larva, right lateral; f, newly-hatched larva, dorsal, × about 127.

(All as seen by reflected light, without compression.)

## Plate XIII.

a, b, c, d, e, *E. hispidarum*; a, b, full-grown larvae, fully extended, dorsal and right lateral, × about 26; c, pupa, dorsal, × about 30; d, e, prepupa, dorsal and left lateral. f, g, *D. javanica*; prepupa, dorsal and left lateral.

(All as seen by reflected light, without compression.)

Plate XIII

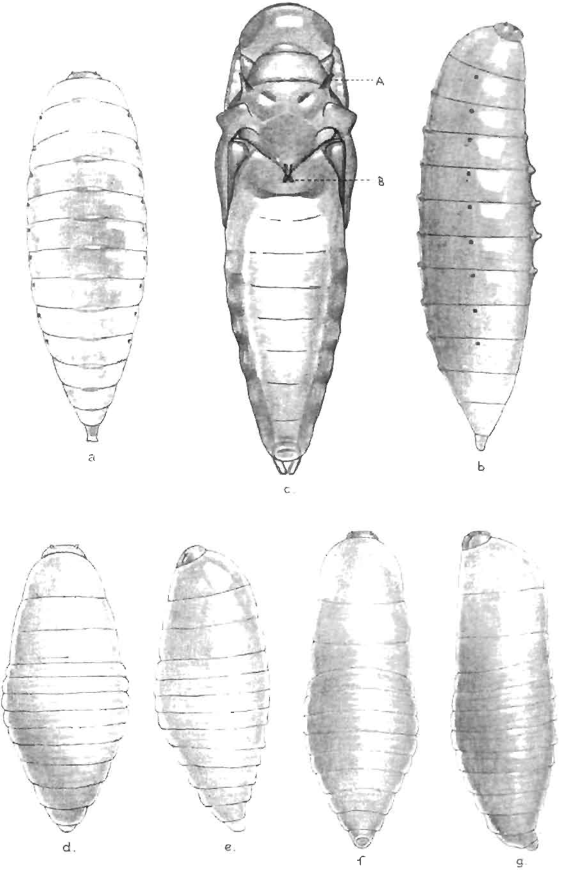
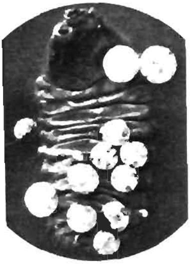
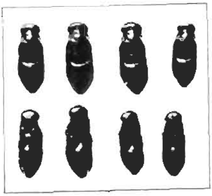


Plate XIV



a.

d.



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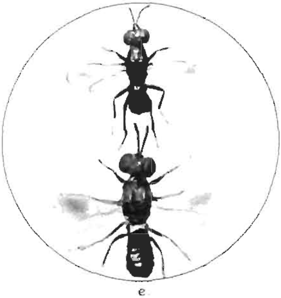

e.

c.

f.

## Plate XIV.

a, *P. ventricosus*, 16 females, most of them mature, but some with spheres still small, feeding on shrivelled larva of *P. reichei*.

b, *P. parvulus*, pupae, dorsal (above) and ventral (below).

c, *D. javanica*, pupae, ventral, showing normal method of attachment to excrement by larval skins.

d, female pupa of *Eupelmus* sp. (left) and of Eupelmid (genus near *Anastatus*).

e, male and female of Eupelmid (genus near *Anastatus*).

f, female of *Eupelmus* sp. (the posterior extremity of the female in e is shown in f, for comparison of lengths of ovipositors).

All × about 9.

## Plate XV.

a, b, c, d, e, *T. taylori*; a, egg, lateral and dorso-ventral, × about 112; b, newly-hatched larva, right lateral, as seen by transmitted light, × about 146; c, prepupa, dorsal and left lateral; d, full-grown larva just after emergence from host, dorsal view, extended, × about 23; e, pupa, dorsal.

f, *D. javanica*, pupa, dorsal.

(All, except b, as seen by reflected light.)

Plate XV.

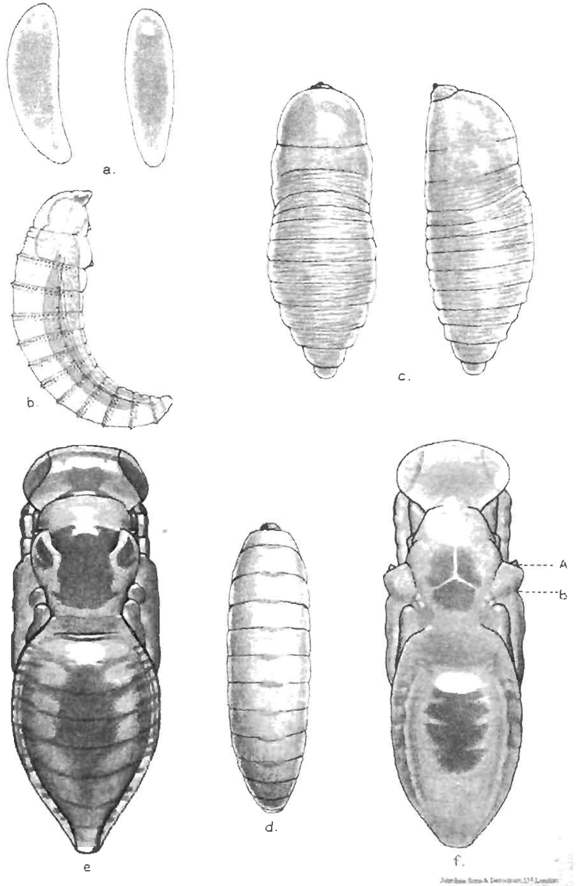

Plate XVI.

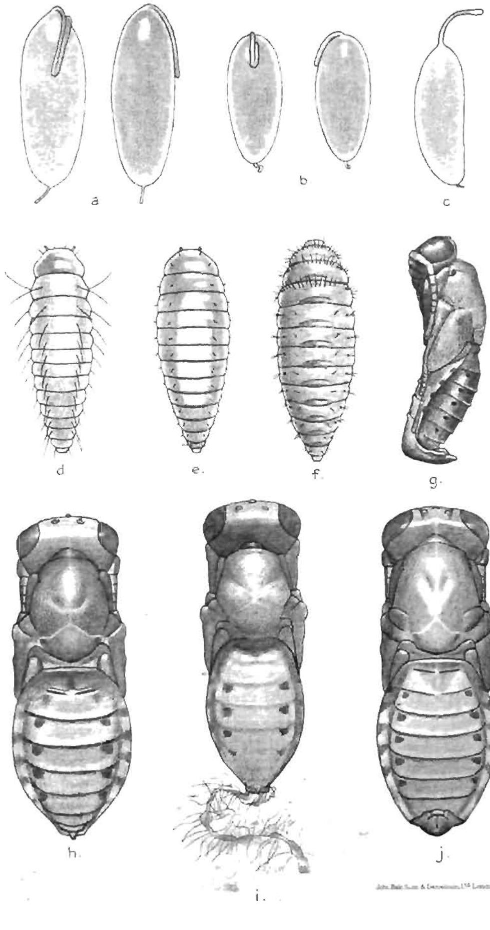


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PLATE XVI.

a, f, g, j, *Eupelmus* sp.; a, 2 aspects of same egg, × 100; f, full-grown (5th-instar) larva, dorsal, × 10; g, pupa, left lateral, × about 13; j, pupa, dorsal, × 20 (g and j, female pupa; male unknown).

b, c, d, e, h, i, *Eupelmid* (genus near *Anastatus*); b, 2 aspects of normal form of egg, × about 67; c, unusual form of egg, with appendage projecting; d, newly-hatched larva, dorsal, × 100; e, 2nd-instar larva, at beginning of instar, dorsal, × 60; h, female pupa, dorsal, × 30; i, male pupa, dorsal, with larval skin still attached, × 30.

(All as seen by reflected light.)

PLATE XVII.

*P. ventricosus*; a, male, × 20; b, female, just after emergence from parent sphere and before commencement of feeding, × about 233; c, female, showing early stage in development of sphere, × about 107; d, mature female, with male waiting at posterior pole of sphere, × about 107.

Plate XVII.

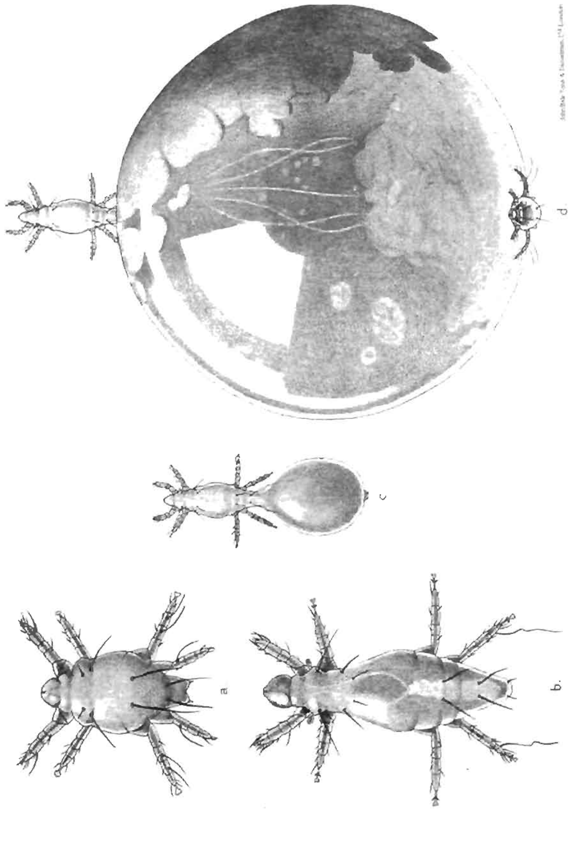

Plate XVIII.

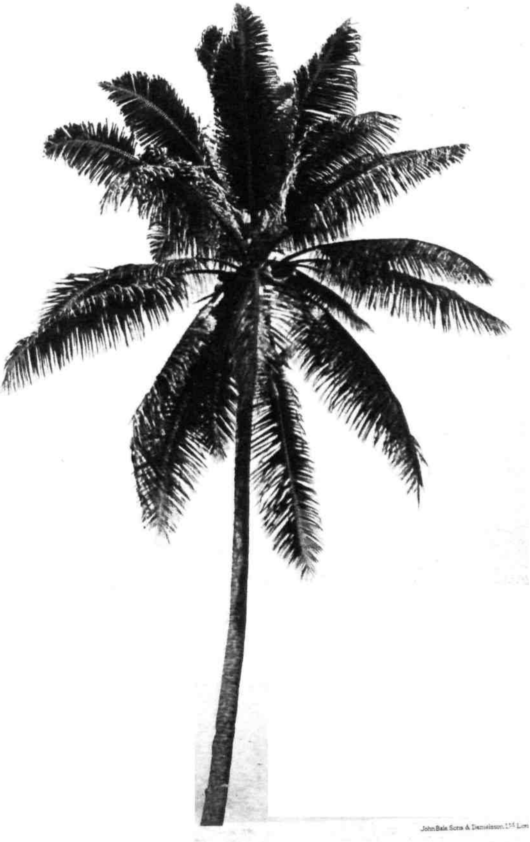

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PLATE XVIII.

Crown of a tall coconut palm, showing typical appearance of damage by *P. reichei* adults, notably the white, curled, extremities of the leaflets of the younger leaves at the top.

## Plate XIX.

Damage done by *P. reichei*.

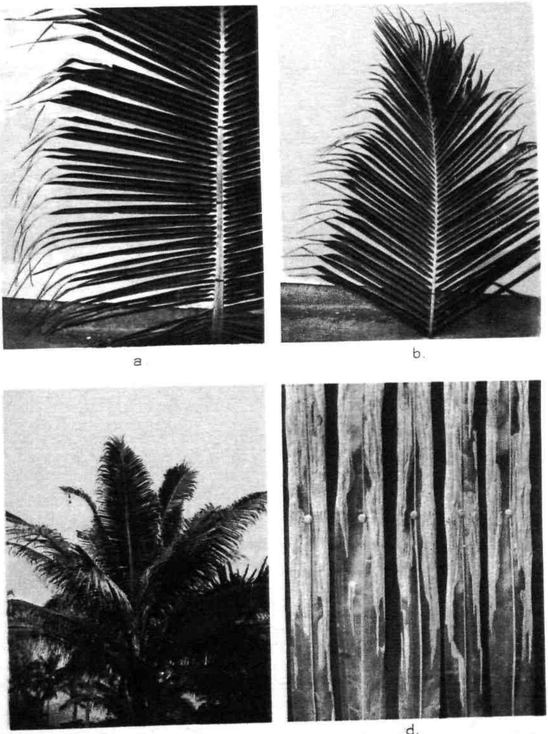
a, underside of proximal half of 5th leaf of severely attacked tree in one-stage outbreak at time when 2nd instar predominated, main stem marked in feet, showing distal thirds of leaflets dead and curled over, owing to damage by beetles, and abundant 2nd-instar mines on all leaflets (visible as dark streaks).

b, underside of distal half of same leaf as a, more reduced.

c, young tree showing ragged appearance, notably curled extremities of leaflets, due to *P. reichei* adults.

d, pupal mines in 5 leaflets from leaf shown in Plate VIII. b (considerably reduced).

Plate XIX.



a. b.

c. d.

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Plate XX

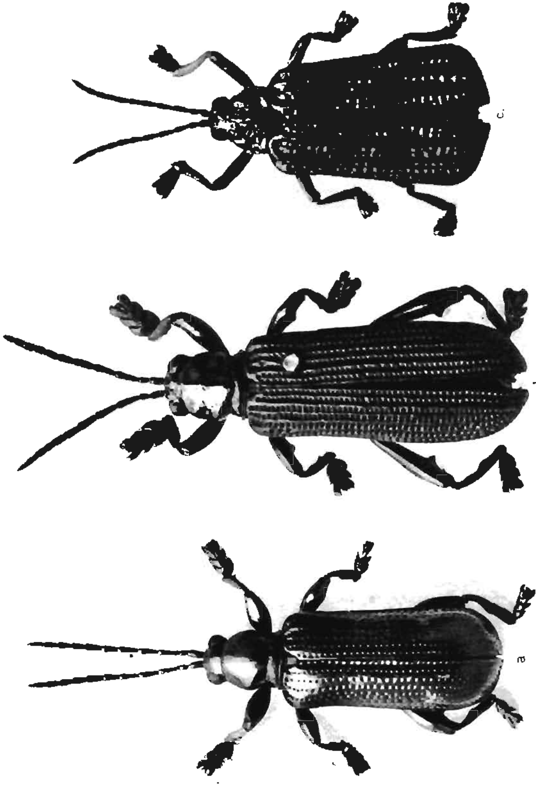

Plate XX.

a, *P. bicolor*, female.
b, *P. nuciferae*, female, elytra slightly apart.
c, *G. xanthomelana*, female, elytra sligbtly apart. All × 9.

PLATE XXI.

*Pleurotropis parvulus*, female, × about 63.

Plate XXI.

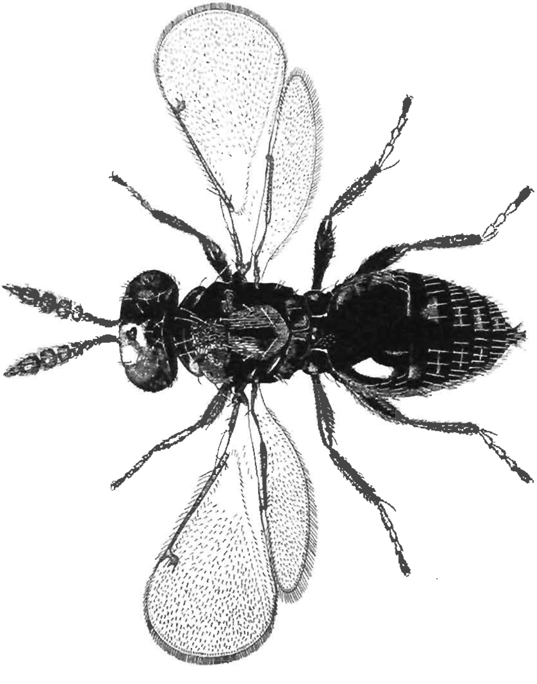

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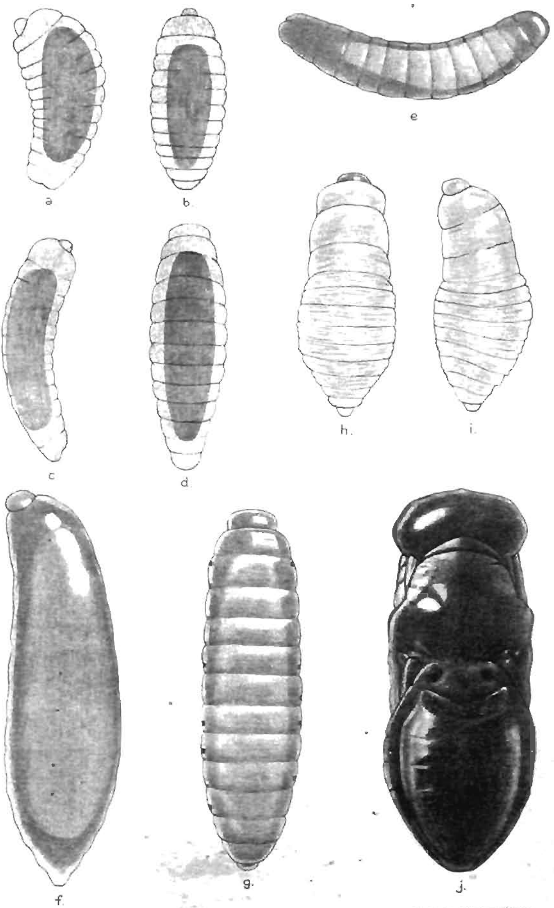
Plate XXII.



## Plate XXII.

*P. parvulus.* a, b, 1st-instar larva, *nearly full-grown for that instar*, left lateral and dorsal views, × about 108 (*cf.* text-fig. 15).

c, full-grown 1st-instar larva, about to moult, right lateral, × about 99.

d, 2nd-instar larva just after moult, dorsal, extended, × about 73.

e, 2nd-instar larva, half-grown for that instar, left lateral, extended, × about 73.

f, full-grown (4th-instar) larva, fully extended, left lateral, × about 32.

g, 4th-instar larva just after moult, dorsal, extended, × about 49 (showing asymmetry of spiracles).

h, i, prepupa, dorsal and left lateral.

j, pupa, dorsal, × about 49.

(a, b, c, and d, as seen by transmitted light, without compression; others as seen by reflected light.)

## Plate XXIII.

*P. parvulus*. a and b, normal appearance of parasitised host larvae at different stages after death; a, larva on left just killed, pale in colour, and just beginning to show blotchy appearance, larva on right at slightly later stage, blotches extensive and nearly black; b, larva on left almost wholly black (but contents were not yet completely devoured and skin was still soft), larva on right black throughout (contents were completely devoured and skin was beginning to dry), with bulges caused by contained parasites, which were prepupae at the time; all 4 larvae in a and b were 2nd instar.

c, three 2nd-instar larvae of *P. reichei* parasitised by *P. parvulus*, as seen when light shines through them, showing (left and centre) pupae of the parasite (in silhouette) in situ and (right) emergence holes and pupal skins (visible as black masses) of the parasites.

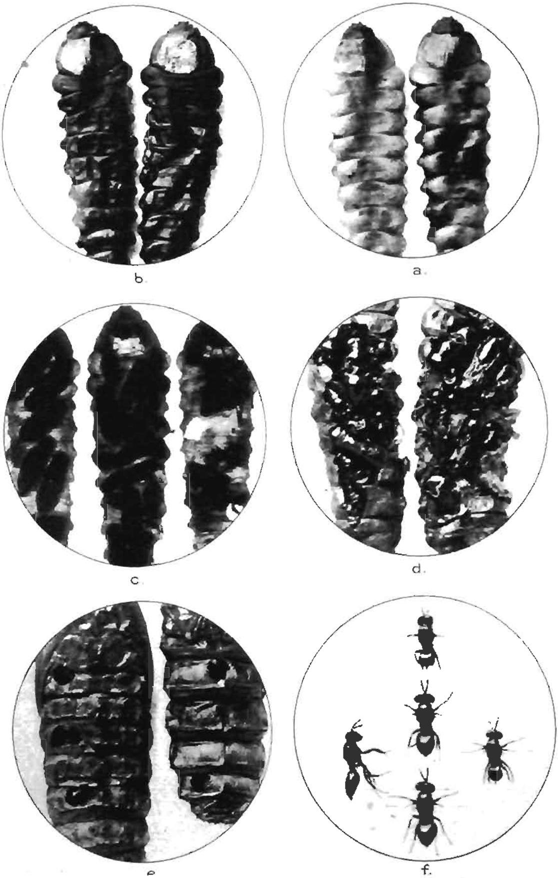
d, pupae of *P. parvulus* in situ in 3rd-instar *P. reichei* larvae, the skin of which has been partly removed to show the parasites.

e, emergence holes of *P. parvulus* adults in pupa of *P. reichei* (dorsal, left, and ventral, right).

f, 2 males (top and right) and 3 females of *P. parvulus*.

All × about 9.

Plate XXIII

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